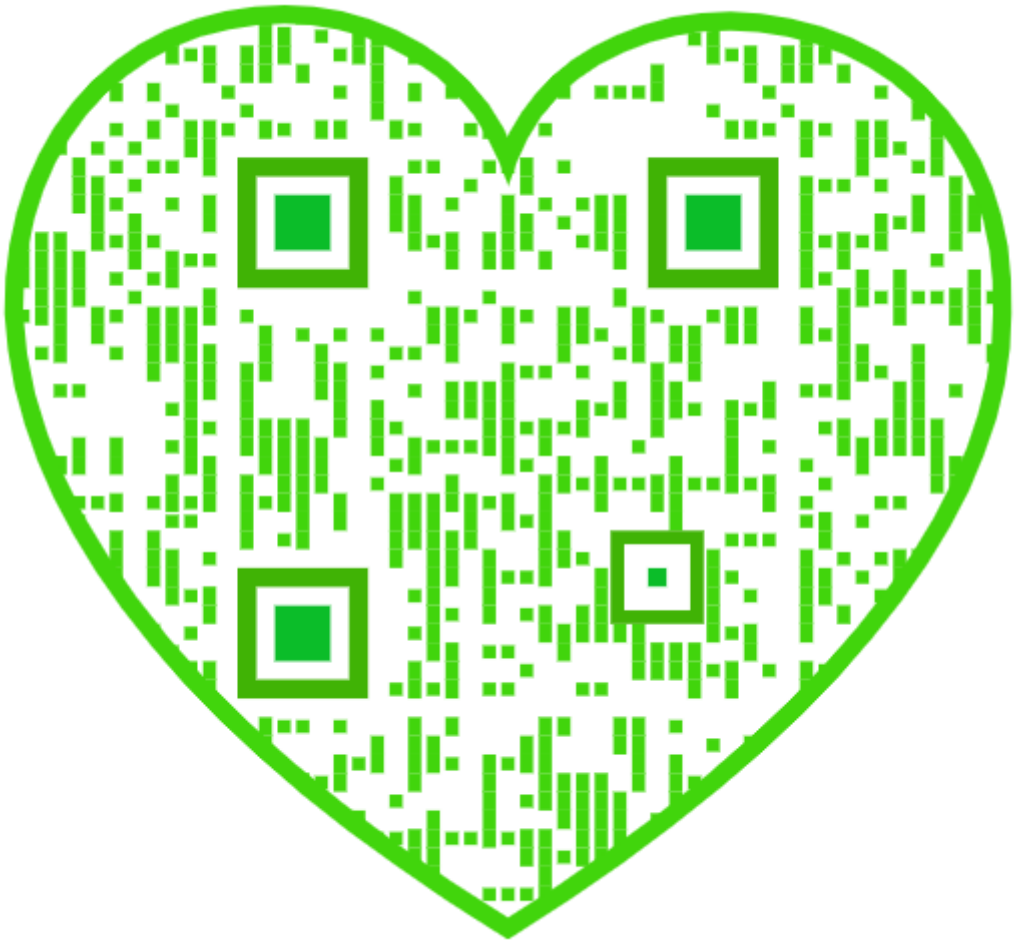

ANNALS OF BOTANY

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ASSISTED BY OTHER BOTANISTS

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„ — BERTHAULT: Observations relatives à la création des prairies.
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„ 85. FRANCHET: Genera nova Graminearum Africæ tropicæ occidentalis.
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„ 3. BOURQUELOT: Sur la composition du grain d'amidon.
„ 4. BERTHELOT: Sur la fixation directe de l'azote gazeux de l'atmosphère par les terres végétales.
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„ — MER: De la formation du bois rouge dans le Sapin et le Picéa.
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„ — ARLOING: Les spores du *Bacillus anthracis* sont réellement tués par la lumière solaire.
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„ 16. CLAUDON ET MORIN: Produits de fermentation du sucre par la levure elliptique.
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„ 19. ARNAUD: Dosage de la Carotine contenue dans les feuilles des végétaux.
„ 20. RIVIERE: De quelques bois fossiles trouvés dans les terrains quaternaires du bassin parisien.
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„ — WILLE: Kritische Studien über die Anpassungen der Pflanzen an Regen und Thau.
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„ — AMBRONN: Zur 'Erwiderung' des Herrn Wortmann.
„ — DAFERT: Uber Stärkekörner welche sich mit Jod roth färben.
„ — DIAKONOW: Lebenssubstrat und Nährsubstanz.
„ 3. CAMPBELL: Zur Entwicklungsgeschichte der Spermatozoiden.
„ — TSCHIRCH: Untersuchungen über das Chlorophyll.
„ — FISCH: Ueber die Zahlenverhältnisse der Geschlechter beim Hanf.
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„ — LINDNER: Ueber Durchwachsungen an Pilzmycelien.
„ — OLIVER: Ueber Fortleitung des Reizes bei reizbaren Narben.
„ 5. MEYER A.: Zu F. W. Dafert's 'Ueber Stärkekörner welche sich mit Jod roth färben.'
„ — KLEBS: Beiträge zur Physiologie der Pflanzenzelle.
„ — REINSCH: Eine neue *Vaucheria* der Corniculatæ, sowie über gynandrische Bildung bei *Vaucheria*.
„ — BACHMANN: Emodin in *Nephroma lusitanica*; ein Beitrag zur Chemie der Flechten.

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„ — CALLMÉ: Ueber zweigliedrige Sprossfolge bei den Arten der Gattung *Carex*.

„ — HABERLANDT: Ueber die Lage des Kernes in sich entwickelnden Pflanzenzellen.

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„ 8. SCHULZE: Bilden sich Nitrate im Organismus höherer Pflanzen?

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——— : Die pelagischen Diatomaceen der Ostsee.

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„ 19. BAUMGARTEN: Ueber die Färbungsunterschiede zwischen Lipra- und Tuberkelbacillen.

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———: Quantitative Bestimmung einiger im Boden vorhandenen absorptiv gebundenen Basen (Kali, Kalk, Magnesia), und Versuche ueber die Frage ob die Pflanze nur gelöste und absorbirte, oder auch stärker gebundene unlöslichere Nährstoffe aufnehmen kann.

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„ — ——————: vi. Mauritius Hemp.

„ 4. FIBRE PLANTS: vii. Manila Hemp (*Musa textilis*, Nees).

„ — ——————: viii. Plantain and Banana fibre (*Musa Sapientum*, R. Br.).

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„ 5. FIBRE PLANTS: x. Bowstring Hemp.

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„ 507 contains descriptions of *Xanthoceras sorbifolia*, *Lapeyrousia grandiflora*, *Corydalis Kolpakowskiana*, *Begonia cyclophylla*, *Ceropegia Monteiroæ*.

„ 508 contains descriptions of *Clavija Ernstii*, *Heuchera sanguinea*, *Chrysanthemum multicaule*, *Hedysarum microcalyx*, *Momordica involucrata*.

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ALMQVIST: Botaniska iakttagelser från sommaren 1885.

HÄFT 2. NATTSÉN: Förteckning öfver Fanerogamer och Ormbunkar, funna inom Alingsås pastorat.

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GRÖNVALL: Tvenne för svenska nya *Orthotricha.*

LINDBERG: Genmåle.

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Den för europas flora förut okända *Potamogeton vaginatus*. Turcz.

AURIVILLIUS: Anteckningar om blomman och befruktingen hos *Aconitum Lycoctonum* L.

ALMQUIST: Några *Carex riparia* liknande former.

HÄGERSTRÖM: Atskilliga former af *Quercus Robur* och *sessiliflora* i norra Skåne.

WITTROCK: Om ett subfossilt, humusbildningen af alger bildadt jordlager, i närheten af Stockholm.

GREVILLIUS: Jakttagelser rörande stipelslidan hos några *Polygonum*-alter.

SKÅRMAN: Bidrag till *Salix*-formationernas utvecklingshistoria på Klarelfvens stränder.

HEFT 3. BAUDIN: *Bryum angustifolium* n. sp.

CALLMÉ: *Carex flava* L. *Marssoni* Auersw.

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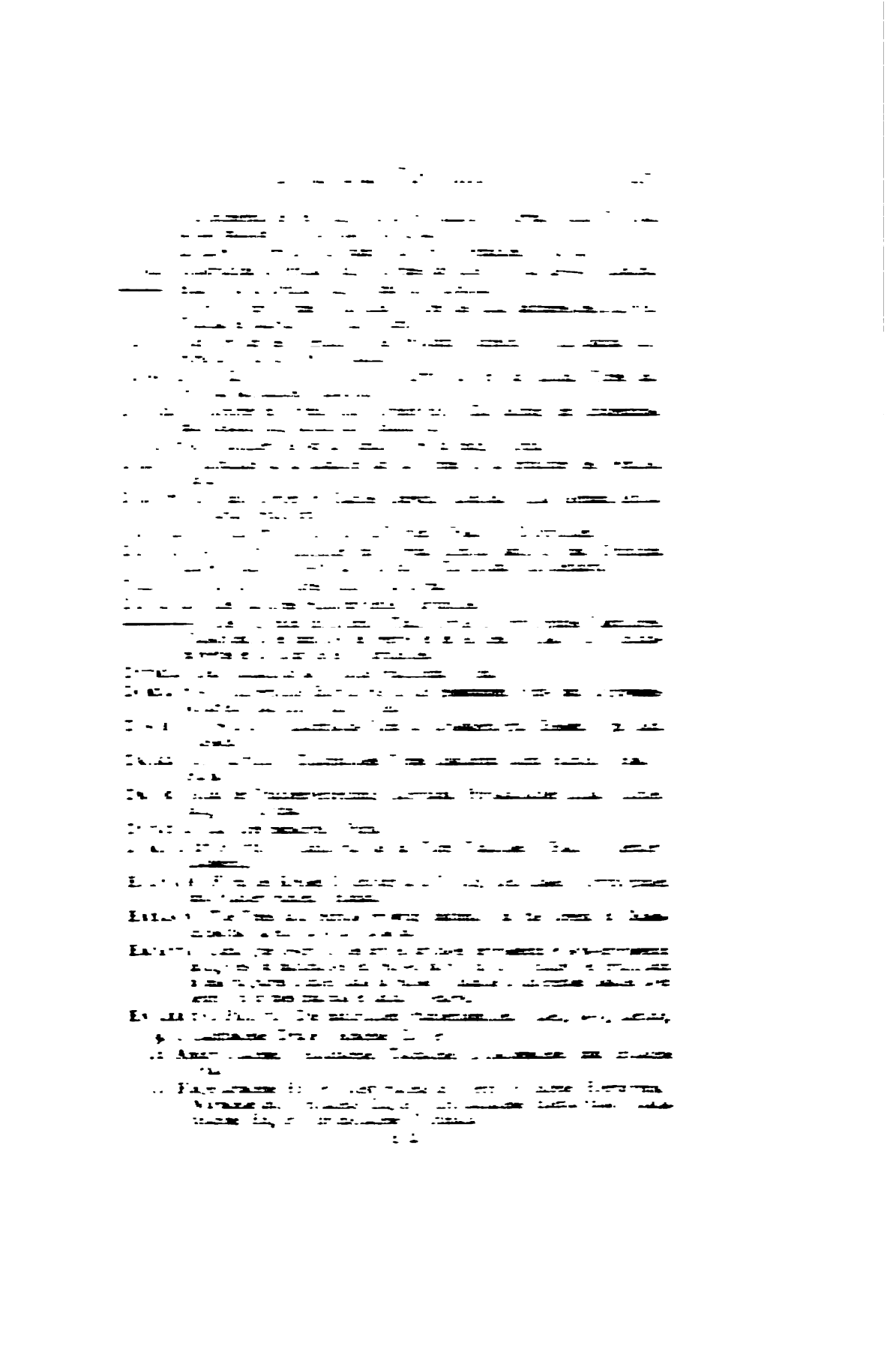

12. Gramineae (Hackel).

13. Angiospermae, Typhaceae (Engler); Pandanaceae (Graf zu Solms); Sparganiaceae (Engler).

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„ — PHILIBERT: *Bryum labradorense*, n. sp.

„ — VENTURI: *L'Orthotrichum Rogeri*, Brid.

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„ — WEBER: *Didymodon subalpinus*.

„ 6. PHILIBERT: Études sur le peristome. VI.

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„ 9. MIQUEL: Instructions sur l'analyse micrographique des eaux.

„ 11. GIRARD ET MIQUEL: Sur l'analyse micrographique des eaux.

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„ — FRITZ MÜLLER: Keimung der *Bicuiba*.

„ — FRANK: Ueber Ursprung und Schicksal der Salpetersäure in der Pflanze.

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„ 13. REIMER UND WILL: Ueber die Bestandtheile des Rüböls.

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„ — JAHNS: Ueber das Trigonellin.

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„ 11. WIGAND: *Nelumbium speciosum*. — Nach des Verfassers Tode herausgegeben von Dr. E. Dennert.

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„ — ZIMMERMANN: Die *Peronospora*-Krankheit des Weinstocks, le mildiou ou le faux *Oidium* américain, the American grape-vine Mildew.

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„ 34. LE NOBEL: Zur Liebermannschen Eiweissreaktion.

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„ 3. SIBER: *Nymphaea Zanzibariensis*, Casp. *Fl. rubro*, Sib.
„ — ENGLER: *Culcasia Mannii* (Hook, f.), Engl.
„ — KOOPMANN: Neuere Orchideen (*Cypripedium Godefroyæ*, Godefr. Leboeuf; *Masdevallia Schlimii*, Lindl.; *Cattleya calumniata*, Rchb. f.).
„ — REGEL: *Heterotoma lobelioides*, Zucc.
„ 4. SPRENGER: *Pogogyne nudiuscula*, Asa Gray.
„ — TSCHAPLOWITZ: Ueber das Grösserwerden der Blätter im Norden.
„ — WIEHLE: Ueber das Einschrumpfen der Knospen bei *Cyclamen*.
„ — BREDEMEIER: *Pinus insignis*, Dougl.
„ — LEHMANN: *Odontoglossum Roezli*, Rchb. f.
„ 5. STEIN: *Strophanthus Ledienii*, Stein.
„ — RÜPPEL: Nomenklatur der Coniferen.
„ 6. REGEL: *Strobilanthus attenuatus*, Jacquemont.
„ — WITTMACK: August Wilhelm Echler.
„ — SCHARRER: Der Dselkwa-Baum, *Zelkowa crenata*, Spach.
„ 7. REGEL: *Iris lineata*, Foster, und *Iris vaga*, Foster.
„ — MÖNKEMEYER: Alphabetisches Verzeichniss sämmtlicher im Monat Januar 1887 beschriebenen neuen oder abgebildeten älteren Pflanzen (the same for February in No. 9, March in No. 11, April in No. 13, May in No. 15, June in No. 17, July in No. 19).
„ 8. DE CANDOLLE: Ursprung des Weizens (*Triticum vulgare*).
„ — BEISSNER: Zur Koniferennomenklatur.
„ — MARSCHNER: *Polygala latifolia*, Ker (*grandis*, Hort.).
„ 9. GRAEBENER: Noch einmal die *Nymphaea Zanzibariensis*, Casp., var. *Fl. rubro*.

Gartenflora (*continued*).

Heft 10. GOETHE: Weitere Beobachtungen über den Apfel- und Birnenrost, *Fusicladium dendriticum* (Wallr.), Fuckel, und *F. pyrinum* (Sib.) Fuckel.
„ 11. REGEL: *Saxifraga longifolia* × *Cotyledon*, Regl.
„ — BEISSNER: Zur Koniferenfrage.
„ — BREDEMEIER: *Abies bracteata*, W. Hook.
„ 12. REGEL: *Oncidium ñians*, Lindl. und *Odontoglossum bictonienſe*, Lindl. *β speciosum*.
„ — STEIN: *Picea alpestris*, Brügger.
„ — WITTMACK: Eine abnorme Fuchsie.
„ — ———: Zapfenkolonie an einer Seestrandskiefer, *Pinus Pinaster*.
„ 13. REGEL: *Allium elatum*, Regl.
„ — KNY: Die Ameisen im Dienste des Gartenbaues.
„ — MAGNUS: Beobachtung des Auftretens zweier Pilzarten, die die Champignonkulturen bei Berlin beeinträchtigen.
„ — REGEL: *Betula Medwedewi*, Regl. und *B. Raddeana*, Trautv.
„ 14. REICHENBACH: *Dendrobium infundibulum*, Lindl.
„ — GAERDT: *Cassia floribunda*, Cav.
„ 15. GARCKE: Über einige Arten der Gattung *Anoda*.
„ ZABEL: *Acer platanoides*, Linn. var. *integrilobium*, Zbl. (nicht Tausch.)
„ 16. DRUDE: *Chionodora Luciliae*, Boiss., und *Ch. sardensis*, Hort.
„ 17. LEHMANN: *Odontoglossum crispum*, Lindl. (*O. Alexandrae*, Bateman).
„ — DRUDE: *Pritchardia Thurstoni*, F. v. M. et Dr. (n. sp.).
„ 18. GRAEBENER: *Rhododendron virgatum*, Hook. fil.
„ — BORNSTEIN: Die Frühjahrs- und Sommerfröste.
„ — ———: Die Schlangenfichte, *Picea excelsa*, Lk., var. *virgata*, Caspary, in Norwegen.
„ — REGEL UND SCHMIDT: Neue und empfehlenswerthe Pflanzen (*Centaurea Clementei*, Boiss., *Crucianella stylosa*, Trin., *Hoya longifolia*, Wall, var. *Shepherdi*, N. E. Brown).
„ 19. GAERDT: *Luculia gratissima*, Sweet.
„ — HERMANN: Ueber die Blüten-Entwicklung einer *Agave filifera*, Salm-Dyck.
„ — KOOPMANN: Die Cultur der Dendrobien.
„ — ———: Luftwurzeln an Birken in Norwegen.
„ — REGEL: *Allamanda cathartica*, var. *Hendersoni*.
„ — HAAGE: *Sarracenia purpurea* und *Dionaea muscipula* auf dem Thüringer Walde.
„ 20. REGEL: *Fritillaria Raddeana*, Rgl., n. sp.
„ — ASCHERSON: *Crucianella stylosa*, Trin.
„ — NIPPERDEY: Die Maulwurfsgrille am Congo.
„ 21. REGEL: *Rhododendron Kamtschaticum*, Pall.
„ — ZABEL: Die Gattung *Symphoricarpus* (continued in Nos. 22, 23).
„ — MÜLLER: *Salix californica*, Hort. (*Salix repens*, L., var. *arenaria*).
„ — ———: *Actinotus Helianthi*, das australische Edelweiss.
„ — REGEL: *Xanthoceros sorbifolia*, Bunge.
„ — ———: *Anomatheca cruenta*, Lindl.
„ — ———: *Carmichaelia Mülleriana*, Rgl., n. sp.
„ — — - : *Masdevallia leontoglossa*, Reichb. fil.

Gartenflora (*continued*).

No. 21. JENSEN: Alphabetisches Verzeichniss sämmtlicher im Monat August, 1887, beschriebenen neuen oder abgebildeten älteren Pflanzen, mit kurzen Beschreibungen.

„ 22. REGEL: *Leucojum autumnale*, L., und *Scilla lingulata*, Poir.

„ — ZABEL: Der australische Weihnachtsstrauch, *Ceratopetalum gummiferum*, Smith.

„ — ———: Noch eine Blume für australische Weihnachtskarten, *Blandfordia nobilis*, Smith.

„ — KASSNER: Betrachtungen über das Mark der Holzgewächse.

„ 23. REGEL: *Stellera* (*Wickströmia*) *Alberti*, Rgl.

„ — ———: *Nidularium Makoyanum*, Rgl., n. sp.

„ — ———: *Eucalyptus piperita*, Smith.

„ — ZABEL: *Betula verrucosa*, Ehrh., var. *laciniata*.

„ — ———: Alphabetisches Verzeichniss sämmtlicher im Monat September, 1887, beschriebenen neuen oder abgebildeten älteren Pflanzen, mit kurzen Beschreibungen.

„ 24. WITTMACK: *Combretum coccineum*, Lam. (*Poivrea coccinea*, DC.)

Hedwigia. Bd. XXVI (*continued*).

Heft 4, 5. HAUCK: *Choristocarpus tenellus* (Kütz.), Zanard.

„ — KARSTEN: Fragmenta mycologica, XXII.

„ — STEINHAUS: Fungi nonnulli novi.

„ — SANIO: Bryologische Fragmente, II (continued in No. 6).

„ — ———: Ueber das Vorkommen der *Chara intermedia*, A. Br. bei Lyk in Preussen.

„ 6. PAZSCHKE: Dr. Georg Winter.

„ — SCHULZER: Vier neue Arten aus den Fungi Slavonici adhuc ineditae.

Jahrbücher, Botanische (**Engler**). Bd. IX.

Heft 1. LIERAN: Ueber die Wurzeln der Aroideen.

„ — PAX: Beiträge zur Kenntniss der Capparidaceae.

„ — ARESCHOUG: Betrachtungen über die Organisation und die biologischen Verhältnisse der nordischen Bäume.

„ — CHRIST: *Spicilegium canariense* (continued in No. 2).

„ — MARLOTH: Die Narras. *Acanthosicyos horrida*, Welw., var. *namaquana*, mihi.

„ — SCHUMANN: Die Flora der deutschen ost-asiatischen Schutzgebiete.

„ 3. PRANTL: Beiträge zur Morphologie und Systematik der Ranunculaceen.

„ — WARMING: Neuere Beiträge zur Flora Grönlands.

„ — KRONFELD: Beiträge zur Kenntniss der Wallnuss (*Juglans regia*, L.).

„ — HILLEBRAND: Vegetationsformationen der Sandwich-Inseln.

„ — KRÄNZLIN: Orchidaceae herbarii Dom. T. Arechavaletae determinatae et descriptae.

Tharander Forstliches Jahrbuch. Supplemente. Bd. IV, Heft 1.

KUNZE: Ueber den Einfluss der Anbaumethode auf den Ertrag der gemeinen Kiefer.

Geographisches Jahrbuch (**Wagner**). Vol. XI.

DRUDE: Bericht über die Fortschritte in der Geographie der Pflanzen.

Jahrbuch der Preussischen Geol. Landesanstalt. Berlin, 1887.

BORNEMANN: Geologische Algenstudien.

Jahrbücher, Landwirthschaftliche. Bd. XVI (*continued*).

WOLFF UND KREUZHAGE: Vegetationsversuche in Sandkultur über das Verhalten verschiedener Pflanzen gegen die Zufuhr von Salpeterstickstoff.

KREUSLER: Beobachtungen über die Kohlensäure-Aufnahme und -Ausgabe Assimilation und Athmung der Pflanzen. 2te Mittheilung.

ATTERBERG: Die Beurtheilung der Bodenkraft nach der Analyse der Haferpflanze.

PLATH: Ueber die Nitrification des Ammoniaks und seiner Salze.

FRANK: Bemerkungen zu dem vorhergehenden Aufsatz.

TACKE: Ueber die Entwicklung von Stickstoff bei Fäulniss.

Jahrbücher für Wissenschaftliche Botanik (Pringsheim). Bd. XVIII (*continued*).

Heft 2. SCHUMANN: Beiträge zur vergleichenden Blütenmorphologie.

„ — BOKORNY: Neue Untersuchungen über den Vorgang der Silberabscheidung durch actives Albumin.

„ — SCHENCK: Beiträge zur Kenntniss der Utricularien, *Utricularia montana*, Jacq., und *Utr. Schimperi*, nov. spec.

„ — SONNTAG: Ueber Dauer des Scheitelwachsthums und Entwicklungsgeschichte des Blattes.

„ 3. RODEWALD: Quantitative Untersuchungen über die Wärme- und Kohlensäure-Abgabe athmender Pflanzentheile.

„ — KRABBE: Ein Beitrag zur Kenntniss der Structur und des Wachsthums vegetabilischer Zellhäute.

„ 4. WILLE: Algologische Mittheilung.

„ — NOACK: Der Einfluss des Klimas auf die Cuticularisation und Verholzung der Nadeln einiger Coniferen.

„ — MOEBIUS: Ueber den anatomischen Bau der Orchideenblätter und deren Bedeutung für das System dieser Familie.

Jahresbericht der Naturforschenden Gesellschaft zu Emden. LXX.

DANGER: Die Pflanzen im Jugendleben der einzelnen Menschen und der Völker.

Jahresbericht der Schlesischen Gesellschaft für vaterländische Kultur. Breslau, LXIV.

HIRT: Ueber Hopëin.

POLECK: Ueber aetherisches Oel von *Allium ursinum*, L.

RÖMER: Ueber die Auffindung einer fossilen Flora in Thonen der Kreideformation bei Bunzlau.

———: Ein Blatt der Gattung *Smilax* aus dem diluvialen Kalktuff von Cannstadt bei Stuttgart.

COHN: Ueber einen Band des Herbars, welches J. J. Rousseau in seinen letzten Lebensjahren angelegt hat.

———: Ueber die vorzugsweise im letzten Jahrzehnt bei Menschen und Thieren beobachteten, meist tödtlich verlaufenden Krankheiten, welche durch Einlagerung körniger Pilzconcremente in die degenerirten Gewebe charakterisirt sind.

———: Ueber Tabaschir.

——–: Ueber eine grönländische Thermalalgae.

EIDAM: Ueber die Keimung der Zygosporen von Basidiobolus, sowie über das Verhalten der Zellkerne im Mycel dieses Pilzes und in den Fortpflanzungsorganen desselben.

Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin. 1887 (*continued*).

No. 8. WITTMACK: Pflanzen aus Kamerun.

„ 9. KNY: Versuche über die Frage, ob der auf Samen einwirkende Frost die Entwicklung der aus ihnen hervorgehenden Pflanzen beeinflusst.

Sitzungsberichte der Gesellschaft für Morphologie und Physiologie in München. Bd. I.

HARTIG: Mittheilungen über Pflanzenkrankheiten.

HARTWIG: Ueber Polyspermie.

PETER: Ueber parasitische Algen.

Sitzungsberichte der Niederrheinischen Gesellschaft. I and II.

KÖRNICKE: Ueber die wilde Stammform des Duchu.

KREUSLER: Ueber Assimilation und Athmung der Pflanzen.

POHLIG: Bituminöses Holz im Basalttuff des Unkelsteins bei Remagen.

Untersuchungen aus dem Botanischen Institut der Königl. Akademie zu Münster-in-Westfalen.

MÖLLER: Ueber die Cultur flechtenbildender Ascomyceten ohne Algen.

Verhandlungen des naturhistorischen Vereines der preussischen Rheinlande, Westfalens und des Reg.-Bezirks Osnabrück.

ESSER: Die Entstehung der Blüthen am alten Holze

Correspondenzblatt.

PIEDBOEUF: Ueber devonische Pflanzen im unteren Wupperthale.

Landwirthschaftliche Versuchsstationen. Bd. XXXIV (*continued*).

MAYER: Die Sauerstoffausscheidung einiger dickblättrigen Planzen bei Abwesenheit von Kohlensaüre und die physiologische Bedeutung dieser Erscheinung.

BENECKE: Ricinuskuchen als Verfälschungsmittel.

GAUNERSDORFER: Das Verhalten der Pflanzen bei Vergiftungen speciell durch Lithiumsalz.

PITSCH UND VAN LOCKEREN-CAMPAGNE: Versuche zur Entscheidung der Frage, ob salpetersaure Salze für die Entwicklung unserer landwirthschaftlichen Kulturgewächse unentbehrlich sind oder nicht.

FRICKE: Beschädigung von Garten- und Feldgewächsen durch Hüttenrauch.

MÖLLER-HOLST: *Avena elatior*, eine technische Schwierigkeit (aus 'Dansk Frökonkal').

NOBBE: Ueber denselben Gegenstand.

BOS: Beiträge zur Kenntniss landwirthschaftlich schädlicher Thiere.

RICHTER: Ueber das Oel der *Lallemantia iberica*, Fisch. et Mey.

HITTNER: Die Bakterien der Futtermittel und Samen.

Zeitschrift für Biologie. Bd. XXIV.

BLOCHMANN: Ueber das regelmässige Vorkommen von bakterienähnlichen Gebilden in den Geweben und Eiern verschiedener Insecten.

TAPPEINER: Nachträge zu den Untersuchungen über die Gährung der Cellulose.

Zeitschrift für Biologie (*continued*).

KUHRIEM: Ueber die eiweissparende Wirkung der Cellulose bei der Ernährung der Herbivoren. Entgegnung.

RUTGERS: Haben vegetabilische Eiweissstoffe den gleichen Nährwerth für den Menschen wie die animalischen?

Zeitschrift für analytische Chemie (Fresenius), XXVI.

KNOP: Ueber die Bestimmung des Ammoniaks in Ackererden.

PALM: Ueber die chemischen Reaktionen der Albuminstoffe, etc.

BAUMANN: Ueber die Bestimmung des Ammoniaks im Boden nach der azotometrischen Methode.

GAWALOVSKY: Quantitative Bestimmung des Mineralölgehaltes in verseifbaren Fetten thierischen und vegetabilischen Ursprungs.

SALKOWSKI: Beiträge zu den Untersuchungsmethoden des Leberthrans und der Pflanzenöle.

Zeitschrift für Hygiene (Koch und Flügge).

Bd. II (*continued*).

No. 3. ERNST: Ueber einen neuen *Bacillus* des blauen Eiters (*Bac. pyocyaneus β*) eine Spielart des *Bac. pyocyaneus* der Autoren.

„ — COHEN: Ueber das Reduktionsvermögen der Bakterien.

„ — PFEIFFER: Das Vorkommen der Marchiafavaschen Plasmodien im Blute von Vaccinirten und von Scharlachkranken.

„ — ESMARCH: Der Keimgehalt der Wände und ihre Desinfection.

FRÄNKEL: Untersuchungen über das Vorkommen von Mikroorganismen in verschiedenen Bodenschichten.

Bd. III.

No. 1. PETRI: Eine neue Methode, Bakterien und Pilzsporen in der Luft nachzuweisen und zu zählen.

„ — LUSTIG: Bacteriologische Studien über Cholera asiatica.

„ — BORDONI-UFFREDUZZI: Ueber die Cultur der Leprabacillen.

Zeitschrift, Jenaische, für Naturwissenschaft. Bd. XX (*continued*).

Supplement Heft 1.

LIEBSCHER: Mikroskopische Futtermittel-Untersuchung.

KRUKENBERG: Untersuchungen über den chemischen Bau der Eiweissstoffe.

FROMMANN: Ueber Veränderungen der Aussenwandungen der Epidermis-Zellen von *Euphorbia Cyparissias, palustris*, und *mauritanica*.

Supplement Heft 2.

REICHARDT: Ueber den Bitterstoff der Kalmuswurzel.

DETMER: Ueber pflanzliche Handelsprodukte.

ABBE: Ueber neue Mikroskope.

DETMER: Ueber die Einwirkung niederer Temperaturen auf Pflanzen.

LIEBSCHER: Eine neue Theorie der Düngung.

Zeitschrift für Naturwissenschaften (Halle). Bd. LX.

Heft 1. HEUSCHKE: Ueber die Bestandtheile der Scopoliawurzel.

Zeitschrift für Physiologische Chemie (Hoppe-Seyler). Bd. XII.

AMTHOR: Studien über reine Hefen.

STUTZER UND ISBERT: Untersuchungen über das Verhalten der in Nahrungs- und Futtermitteln enthaltenen Kohlenhydrate zu den Verdauungsfermenten.

Zeitschrift für Physiologische Chemie (Hoppe-Seyler) (*continued*).

KELLNER UND YOSHII: Ueber die Entbindung freien Stickstoffs bei der Fäulniss und Nitrification.

EHRENBERG: Nachtrag zu den Untersuchungen über die Entwicklung von gasförmigem Stickstoff bei Fäulnissprocessen.

Zeitung, Botanische. Jahrgang XLV (*continued*).

No. 31–37. WINOGRADSKY: Ueber Schwefelbakterien.

„ 37–39. JOST: Ein Beitrag zur Kenntniss der Athmungsorgane der Pflanzen.

„ 40. KARSTEN: Berträge zur Kenntniss von *Fegatella conica.*

„ 41. TOMASCHEK: Ueber *Bacillus muralis.*

„ — BOEHM: Ueber die Respiration der Kartoffel (continued in No. 42).

„ 43. KLEBS: Einige Bemerkungen zu der Arbeit von Krasser, 'Untersuchungen über das Vorkommen von Eiweiss in der pflanzlichen Zellhaut,' &c.

„ 44. WEHMER: Ueber das Verhalten der Formose zu entstärkten Pflanzenzellen.

„ — GOEBEL: Bemerkung zu der Abhandlung von Jost 'Ein Beitrag zur Kenntniss der Athmungsorgane der Pflanzen.'

„ 45–47. HOFFMANN: Culturversuche über Variation (continued from No. 18).

„ 46. JOHANNSEN: Ueber Fortdauer der 'Athmungs-Oxydation' nach dem Tode.

„ 48–51: WORTMANN: Zur Kenntniss der Reizbewegungen.

„ 52. LÖW UND BOKORNY: Ueber das Vorkommen von activem Albumin im Zellsaft und dessen Ausscheidung in Körnchen durch Basen.

Deutsche Chemiker Zeitung. 1887.

REINSCHE: Wirkung des Pyrofuscins auf Schizomyceten.

GREAT BRITAIN.

The Orchid Album. (**Warner, Williams, and Moore.**)

Vol. VI. contains plates and descriptions of:—*Aërides Lawrencia*, Rchb. f.; *Brassavola Digbryana*, Lindl.; *Cattleya Mardellii*, Rchb. f.; *C. Mossiae*, Hook; *C. speciosissima Buchaniana*, Williams et Moore; *C. Trianae Dodgsoni*, Williams; *C. Trianae Hooleana*, Will.; *C. Trianae Massangeana*, Rchb. f.; *Coelogyne Dayana*, Rchb. f.; *Cycnoches chlorochilon*, Klotzsch; *Cymbidium giganteum*, Wall.; *Cypripedium insigne punctatum violaceum*, O'Brien; *C. selligerum*, Veitch; *Dendrobium Falkoneri giganteum*, Hort.; *D. primulinum*, Lindl.; *D. Treacherianum*, Rchb. f.; *D. Williamsianum*, Rchb. f.; *Galeandra Bauerii*, Lindl.; *Habenaria militaris*, Rchb.f.; *Laelia amesiana*, Rchb. f.; *L. anceps Percivaliana*, Rchb. f.; *L. elegans Wolstenholmiae*, Rchb. f.; *L. purpurea Russeliana*, Will.; *L. superbiens*, Lindl.; *Lissochilus Krebsii purpuratus*, Ridley; *Lycaste Deppei punctatissima*, Rchb. f.; *L. Spinnerii reginae*, Will.; *Masdevallia ignea massangeana*, Will.; *M. roezlii rubra*, Hort.; *Odontoglossum adspersum*, Rchb. f.; *O. cervantesii decorum*, Rchb. f.; *O. Alexandrae reginae*, Hort.; *O. luteo-purpureum magnificum*, Williams et More; *O. pardinum*, Lindl.; *O. polletianum*, Hort.; *Oncidium papilio-majus*, Rchb. f.; *O. stelligerum Ernesti*, Will.; *O. superbiens*, Lindl.; *Phalaenopsis grandiflora*, Lindl.; *Ph. rosea*, Lindl.; *Saccolabium Hendersonianum*, Rchb. f.; *Sobralia leucoxantha*, Rchb. f.; *S. xantho*

The Orchid Album (*continued*).

leuca, Hort.; *Trichocentrum orthoplectron*, Rchb. f.; *Thrixpermum unguiculatum*, Rchb. f.; *Vanda coerulea*, Griffith; *V. Denisoniana herbaica*, Rchb. f.

Vol. VII. contains plates and descriptions of:—*Cattleya Mossiae aurea grandiflora*, Moore; *Vanda cristata*, Lindl.; *Sophronitis violacea*, Lindl.; *Odontoglossum Andersonium splendens*, Williams; *Aërides crispum Warnerii*, Williams; *Odontoglossum luteo-purpureum sceptrum*, Rchb. f.; *Cattleya Wageneri*, Rchb. f.; *Vanda Amesiana*, Rchb. f.; *Acineta Humboldtii*, Lindl.; *Aërides virens Eltisii*, Williams; *Dendrobium polyphlebium*, Rchb. f.; *Angraecum citratum*, Du Petit Thonars; *Cypripedium curyandrum*, Rchb. f.; *C. concolor*, Parish; *Dendrobium densiflorum* Wall.; *Cypripedium Measuresianum*, Will.; *Odontoglossum Pescatorei Germinyanum*, Williams; *Lycaste plena Measuresiana*, Will.; *Cattleya sororia*, Rchb. f.; *Dendrobium formosum giganteum*, Van Houtte; *Aërides Fieldingii*, Lindl.; *Cattleya Eldorado splendens*, Linden; *Coelogyne asperata*, Lindl.; *Dendrobium superbiens*, Rchb. f.

Annals of Botany. Vol. I.

No. 1.

MARSHALL WARD, AND DUNLOP: On some points in the Histology and Physiology of the Fruits and Seeds of *Rhamnus*.

GARDINER AND ITO: On the structure of the mucilage-secreting cells of *Blechnum occidentale*, L., and *Osmunda regalis*, L.

CALVERT AND BOODLE: On laticiferous tissue in the pith of *Manihot Glaziovii*, and on the presence of Nuclei in this Tissue.

GREGG: Anomalous thickening in the roots of *Cycas Seemanni*, Al. Braun.

OLIVER: Phenomenon analogous to leaf-fall.

VAIZEY: The transpiration of the Sporophore of the Musci.

BLAKE: The prickle-pores of *Victoria regia*.

CALVERT: The laticiferous tissue in the stem of *Hevea brasiliensis*.

BALFOUR: 'Sporophore' and 'Sporophyte.'

No. 2.

HOOKER: On *Hydrothrix*, a new genus of Pontederiaceae.

OLIVER: On the obliteration of the Sieve-tubes in Laminariae.

TREUB: Some words on the life-history of Lycopods.

BOWER: On the modes of climbing in the genus *Calamus*.

——— : On the limits of the use of the terms Phyllome and Caulome. A suggestion.

VAIZEY: On the absorption of water, and its relation to the constitution of the cell-wall in Mosses.

MORRIS: On the use of certain plants as Alexipharmics or Snake-bite antidotes.

ROBINSON: Notes on the genus *Taphrina*.

VINES: Apospory in Characeae.

SCHÖNLAND: Method for preserving the colours of Flowers in dried specimens.

——— : The apical meristem in the roots of Pontederiaceae.

BOWER: Preliminary note on the formation of Gemmae on *Trichomanes alatum*.

BALFOUR: 'Coco-nut,' not 'Cocoa-nut.'

Annals and Magazine of Natural History. Series 5. Vol. XIX.

OUDEMANS: *Sporendonema terrestre*, Oudemans, an example of endogenous spore-formation among the Hyphomycetes.

Bulletin of Miscellaneous Information. Royal Gardens, Kew, 1887 (*continued*).

No. 7. xii. Annatto (*Bixa Orellana*, L.).
„ — „ Botanical Stations in West Indies.
„ 8. xiii. Tree Tomato (*Cyphomandra betacea*, De Candolle).
„ — xiv. Chocho (*Sechium edule*, Sw.).
„ — xv. Arracacha (*Arracacia esculenta*, De Candolle).
„ — xvi. Cherimoyer (*Anona Cherimolia*, Mill).
„ 9. xvii. Annatto (*Bixa Orellana*, L.).
„ — xviii. Notes on Articles contributed to Museums of the Royal Gardens, Kew, from the Colonial and Indian Exhibition, 1886.
„ 10. xix. Onion Disease at Bermuda (*Peronospora Schleideniana*, De Bary).
„ 11. xx. Colonial Fruit.
„ 12. xxi. Chubebs (*Piper Cubeba*, L.).
„ — xxii. Sabicù Wood (*Lysiloma Sabicu*, Benth.).
„ — xxiii. Mexican Fibre or Istle (*Agave heteracantha*, Zucc.).
„ — xxiv. Food Grains of India.
„ — xxv. Broom Root or Mexican Whisk (*Epicampes macroura*, Benth.).
„ — xxvi. Contrayerva (*Dorstenia brasiliensis*, L., *Dorstenia contrayerva*, L. *Aristolochia odoratissima*, L.).
„ — xxvii. Introduction of the Brazil Nut to the East Indies and Australia (*Bertholletia excelsa*, Humb.).
„ — „ Castilloa Rubber of Central America (*Castilloa ela tica*, Cerv.).

Agricultural Students' Gazette. Vol. III. Part 3–5.

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No. 511 contains plates and descriptions of *Lonchocarpus Barteri*, *Alpinia zingiberina*, *Tillandsia Jonghei*, *Corydalis Ledebouriana*, *Strobilanthes flaccidifolius*.

„ 512 contains plates and descriptions of *Rhododendron grande*, var. *roseum*, *Escallonia revoluta*, *Narcissus cyclamineus*, *Alseuosmia macrophylla*, *Ipomoea Robertsii*.

„ 513 contains plates and descriptions of *Hillebrandia sandwicensis*, *Barberia repens*, *Coelogyne corymbosa*, *Primula obtusifolia*, *Iris Kingiana*.

„ 514 contains plates and descriptions of *Anemone Fanninii*, *Statice Suworowi*, *Iris Sari*, var. *lurida*, *Primula sapphirina*, *Primula Reidii*, *Dendrobium sulcatum*.

„ 515 contains plates and descriptions of *Landolphia florida*, *Phalaenopsis Mariae*, *Polemonium flavum*, *Morina betonicoides*, *Vicia Denessiana*.

„ 516 contains plates and descriptions of *Anthurium Veitchii*, *Helicophyllum Alberti*, *Rubus rosaefolius*, *Oncidium micropogon*, *Rhododendron rhombicum*.

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„ — NILSSON: Ofversigt af de skandinaviska arterna af slägtet *Rumex* och deras hybrider: *Rumex maritimus*, L., och *R. palustris*, Sm.

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„ — WILLE: Om Topcellevaexten hos *Lomentaria kaliformis*.
„ — ———: Djaevelstidet in bladene hos *Phragmites communis*.
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LEWIN: Bidrag till Hjerbladets Anatomi hos Monokotyledonerna.

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„ 9. HÖGRETT: Bergjums fanerogamer i blomningsföljd.
„ 10. NEUMAN: Om *Rubus corylifolius* och *R. pruinosus* deras nomenklatur.

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FRAGOSO: *Ectocarpus Lagunae*, especie nueva de la costa de Cádiz (Lámma V).
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DE CANDOLLE: Sur l'origine botanique de quelques plantes cultivées et sur les causes probables de l'extinction des espèces.
COAZ: Du développement des plantes phanérogames sur le terrain abandonné par les glaciers.
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BRUNNER ET CHUARD: La présence de l'acide glycosuccinique dans les végétaux.

On some points in the Histology and Physiology of the Fruits and Seeds of Rhamnus.

BY

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ASSISTED BY

JOHN DUNLOP.

With Plates I and II.

SOME time ago my attention was directed to some curious facts about 'Persian Berries,' the fruits of certain species of *Rhamnus* used in dyeing. It had long been known that a beautiful golden yellow solution can be obtained by simply macerating these fruits in water, and various researches on the part of chemists had demonstrated that the dye is obtained chiefly if not entirely from the husks (pericarps); at the same time dyers and others knew that the crushed berries yield a satisfactory colouring matter, whereas the pericarps alone do not. For some reason it is necessary to employ the inner parts of the fruits as well as the pericarps; these inner parts of course include the seed when the berries are crushed whole, as is the usual practice. Various species of *Rhamnus*—*R. Amygdalina*, *R. infectorius* (*R. oleoïdes*[1]), *R. saxatilis*, &c.—are employed as 'Persian Berries,' and although the following remarks apply particularly to *R. infectorius*, there are reasons for believing that they may apply generally to other species also.

[1] Mr. Thiselton Dyer informs me that this is a synonym of *R. Amygdalina*.

[Annals of Botany, Vol. I. No. I. August 1887.]

In 1842 Fleury examined a yellow dye got from the fruits of a *Rhamnus*; a little later Kane obtained a body which was called *chrysorhamnin* from unripe fruits, and another from ripe fruits which he named *xanthorhamnin*. Gellatly in 1851 gave a complex formula (C_{48} H_{56} O_{28}) to this xanthorhamnin, and stated that dilute sulphuric acid causes it to break up into a body called *rhamnetin* and grape-sugar—in other words, that xanthorhamnin is a glucoside. This was confirmed subsequently.

In 1879 Liebermann and Hörmann, employing *R. infectorius*, confirmed the foregoing, and found that no dye (or the merest traces) is obtained from the seeds, but that it exists in the husks (pericarps). They got the glucoside xanthorhamnin, which is soluble in water and alcohol, but not in ether, benzole or chloroform, and assigned to it the formula C_{48} H_{66} O_{29}. It is soluble in alkalies; ferric chloride turned the solution brown. Sulphuric acid causes it to break up into glucose and rhamnetin.

They also found that the xanthorhamnin breaks up under the action of some ferment in the fruit, the products of this reaction being a colouring body, *rhamnin* and glucose.

This was practically the position of our knowledge, when my attention was directed to an experiment performed by Mr. T. E. Lightfoot, of Accrington, a gentleman interested in dyeing, and who was then investigating the qualities of the different yellow dyes obtainable from 'Persian Berries.' Mr. Lightfoot has informed me by letter that he found that a decoction of the uninjured berries yielded a poorer colouring liquor than one obtained from the ground or crushed 'berries.' He then took some of the fruits, and split them, separating the outer shells—the chief part of the pericarp—from the 'kernels'; these 'kernels' are the seeds, and they are covered by a thin hard covering which, as will be seen shortly, is the endocarp.

A weighed quantity of the outer pericarps was then used for making a decoction, and a piece of cloth dyed with the liquor; in another vessel the same weight of 'shells' (pericarp) was used, but a few of the 'kernels' (seeds) added.

In the second case the colouring matter was a brilliant golden yellow, whereas the former gave but a poor lemon-yellow dye.

The outer pericarps were next digested in water at 45°C. for about one hour, and the clear yellow filtered liquor was placed aside with a few 'kernels' (seeds) added; in thirty minutes or so a light yellow powder fell to the bottom, C O_2 being given off meanwhile.

'Kernels' were then split up into four parts, and these parts kept separate. (1) The shell or husk of the 'kernel' (i. e. the endocarp); (2) A greyish white matter (i. e. endosperm); (3) the infolded rims of the seed proper; (4) a yellow substance—the embryo—inside the seed.

To clear decoctions of the outer pericarps Mr. Lightfoot then added the different parts of the dissected kernels, and found that in every case the yellow powder fell after a time, but more quickly where the rims of the seed were added. The action was destroyed by boiling.

The obvious explanation of the above experiments is that a ferment, localised in the 'kernels' (seeds), acts on the yellow substance dissolved from the pericarps.

Having obtained some fruits of *Rhamnus infectorius* from Kew, I set to work to investigate the matter independently.

I found that if the whole fruits are steeped in water, and kept at 35°C., a quantity of bright yellow substance collects around the swollen mass, and if squeezed out gradually forms a slight precipitate. On breaking these steeped fruits there is abundance of glairy yellow substance inside, not easily washed away. If the fruits are broken up *first*, however, a copious precipitate soon falls; this is yellow, and finely crystalline, and is evidently the rhamnin of the chemists[1]. The filtered liquor after this experiment reduces Fehling's solution, and contains relatively large quantities of glucose.

I then repeated the experiments with the various parts of

[1] Husemann, 'Pflanzen-stoffe,' vol. ii. 1884, p. 889, where the chemical literature is quoted.

the seeds and the endocarp. The chief difficulty here was to obtain perfectly clean portions. It was easy to separate the endocarp; far less easy to separate the testa of the seed from the contents. The large yellow embryos slip out pretty easily. I doubt whether the testa was ever got perfectly free from the nucellus in these earlier trials. A decoction of the freed outer pericarps was then made, and the clear yellow filtered solution placed in test-tubes and treated as follows:—

A: was left alone.
B: testa was added.
C: endocarp was added.
D: endosperm was added.
E: embryo was added.

All the experimental tubes were placed in a warm chamber and kept at 35°C. After half-an-hour I found a copious yellow crystalline precipitate falling in B, and faint traces of a similar precipitate in E. In all the other tubes the liquid was still clear. After eight to twelve hours traces of a precipitate were observable in the other tubes, but it was more than a day after that any noteworthy changes were observable.

Evidently something in the testa (and possibly in the embryo also) acts as a ferment on the yellow glucoside in the pericarp. I repeated the experiment B, but boiled the solution after adding the testa; a coarse cloudy precipitate formed. It became probable later that this was due to the boiling. I again repeated experiment B, with the following modifications. In one case I employed a glycerine-extract of the testa; this was effectual, as before. In another case I used a filtered water-extract of the testa; this was effectual also, but *not so if boiled first.* There seemed to be a soluble ferment in the testa of the seed then, and it is obvious that the results confirmed previous experiments.

It was now time to examine the tissues histologically, and I confined my attention at first to the testa and pericarp. In the cells of the outer pericarp are brittle waxy yellow masses (Fig. 6), which dissolve at once in water, and are evidently masses of the glucoside (xanthorhamnin). The

testa contains thick-walled pitted cells (Figs. 4 and 12) which contain a peculiar finely granular substance, which dissolves at once on adding water and disappears. I was for some time strongly inclined to regard this fine grey powder as the ferment with which we had been experimenting. To test the accuracy of this conclusion I made very thin sections of the dry testa, and placed them directly into solutions of the glucoside from the pericarp; the sections were from all parts of the testa. In less than half-an-hour I found a semi-crystalline precipitate resembling the precipitates of rhamnin obtained in the test-tubes.

I then asked Mr. John Dunlop, who was at that time working in my laboratory at the Owens College, to go over the anatomy and histology of the fruits and seeds of *Rhamnus* with me; this he was good enough to do, and most of the figures in the plates are due to his pencil. We confined our attention to *Rhamnus infectorius* at the time; later on I examined the histology of several other species.

The fruit of *Rhamnus infectorius* is a berry-like drupe (Fig. 1) with a dry waxy outer pericarp, and a thin woody endocarp: within this are three or four erect seeds, which, if separately and completely enclosed in the sclerenchymatous endocarp, might almost be called nutlets (Fig. 2). A horizontal transverse section made equatorially across the drupe reveals the seeds lying loosely in the loculi of the dry fruit, one in each loculus, enclosed in the hard thin endocarp. On splitting this endocarp the seeds fall out, being loose within it; each seed is smooth and shining, brown in colour, and with a longitudinal deep groove on the dorsal side. A transverse section of the seed shows a hard brown testa, doubled in at the dorsal groove (Figs. 3 and 21), the margins of the groove being thickened and harder than the rest. The cavity within the testa is nearly horseshoe-shaped in transverse section, and filled with white endosperm, in which lie the cotyledons: these are face to face and also horseshoe-shaped in transverse section. Between the endosperm and testa were several rows of broken down and disorganised cells, evidently

the remains of the nucellus. In the dry state all the parts are shrunken, and a large hollow cavity exists on the dorsal side of the endosperm—between it and the testa. The various parts of the fruit were then separated and sections cut so as to exhibit their structure. The outer pericarp is brittle and waxy in texture: their sections, in the dry state, show (Fig. 5) an outer epidermal layer, the external cell-walls of which are strongly cuticularised. With the exception of certain small granules, looking very like plastidia, these cells and those immediately below them have no contents. Immediately below the epidermal layer are four or five rows of hypodermal cells, the outer rows consisting of regular rectangular cells, which in the inner rows become less and less regular and smaller, all however containing small corpuscles near the interior of their walls. These seem to be chlorophyll-corpuscles. Below these cells are larger, thin-walled, parenchymatous cells containing a yellow amorphous substance which completely filled up the cavity of the cell (Figs. 5 and 6).

Water was then added to the dry sections while still under the microscope; the cell-walls, etc. swelled up and the yellow substance in the cells at once dissolved completely, colouring the water yellow and leaving the cavities of the cells empty; the latter were then seen to be thin-walled and parenchymatous (Fig. 5).

To other dry sections under the microscope glycerine was added; they again swelled up and the yellow substance in the parenchymatous cells again dissolved, but not so rapidly as in water. Sections were treated in a similar manner with alcohol, chloroform and ether; the yellow substance dissolved to a very slight extent in alcohol, but was insoluble in chloroform and ether. Thus the yellow substance was not a wax, resin or fat, any of which would probably have dissolved in any of the last three reagents, and not in water or glycerine.

The histology of the endocarp was next made out. Its inner yellow lining was stripped off and examined; it was found to consist of a layer of long thin-walled cells containing a yellow waxy-looking substance, and on adding water the

contents cracked and dissolved like the substance contained in the cells of the outer pericarp, leaving the cell cavities empty and allowing the shape of the cells to be more clearly seen (Figs. 8 and 9). On treating dry sections with glycerine, the yellow substance again dissolved, but more slowly than in water (Fig. 8). This yellow substance was treated with alcohol, chloroform and ether, and acted in the same way as the yellow substance in the parenchyma cells of the outer pericarp. Transverse sections were then cut of this inner husk, and the cells appeared rectangular, the cell-wall being slightly thickened on the exterior surface (Fig. 10).

As regards the rest of the endocarp, thin transverse sections were cut, and were found to consist of a number of rows of hard sclerenchymatous cells, of which the lumina were nearly obliterated, having a very distinct middle lamella between the cells, and with a large number of pits radiating from the lumina to the middle lamella, corresponding to pits radiating from the lumina of contingent cells (Fig. 7).

Thin transverse sections of the testa were then cut, and it was found to consist of a single row of sclerenchymatous cells, with a number of pits radiating from the centre of each lumen, the cell-cavity containing a greyish substance which diffused out of the cell on adding water to the section. The middle lamella of the cell-wall was very well marked (Figs. 11 and 12).

Thin tangential sections of the endosperm were cut, the tissue was found to consist of thin-walled parenchyma, the cells containing protoplasm and various other bodies. On adding water to the sections oily drops separated out in the cells, and exuded at the sides of the sections; the water was then removed and alcohol added, the fatty drops disappeared (Fig. 14). Fresh sections were cut and placed dry in alcohol and examined in glycerine, the fat had dissolved and a number of small grains closely packed were left in the cells. Sections which had been treated with alcohol as before were examined and water added while under the microscope, and these grains dissolved after swelling up. Thus the endosperm contained

fats and grains which there were grounds for thinking were aleurone grains. To confirm this supposition sections were cut and placed in a two per cent. solution of mercuric chloride in absolute alcohol, and were left in it for about forty-eight hours, washed for half a minute in water, stained rapidly with eosin, and mounted in a solution of a neutral salt, potassium acetate being used. On examining the sections a large number of aleurone grains were found in the cells, but on examining the grains no enclosure could be detected within them (Fig. 15). Sections were placed in the alcoholic solution of mercuric chloride as before and left for twenty-four hours, then washed in absolute alcohol, stained rapidly with eosin, washed for half a minute in water, and mounted in a solution of potassium acetate. On examining these sections it was found that the aleurone had been dissolved out by washing in the water, leaving a reticulum of protoplasm in which the aleurone grains had been lying, and showing a well-stained nucleus in each cell (Fig. 16).

Sections of the cotyledons were cut and examined dry, they were a light yellow in colour; on adding water the cells became more distinct, and oily globules separated out, which on removal of the water dissolved in alcohol, chloroform and ether. The sections consisted of about six or seven rows of cells, the outer row on each side being arranged very regularly and with their outer walls slightly thickened. The second row on the one side consisted of columnar cells, while those in the centre were more irregular and larger, and with a number of intercellular spaces between them (Fig. 17).

Sections were treated with the alcoholic solution of mercuric chloride for twenty-four hours, washed for half a minute in water, stained with eosin and mounted in a solution of potassium acetate. On examining the sections it was found that the cells contained a large amount of aleurone, which seemed to be similar to that contained in the endosperm, as no enclosure could be detected within the grains which, on the addition of water, swelled up and dissolved.

The cells of the embryo are thin-walled and parenchyma-

tous, containing protoplasm, aleurone and fats, together with a yellow substance, the nature of which I was unable to make out, but which did not seem to be identical with the yellow substance contained in the outer pericarp and endocarp, and this supposition was strengthened by the action of the various parts on one another, this yellow substance contained in the cotyledons not acting in the same way as the yellow body contained in the pericarp and endocarp.

On cutting sections of the embryo and staining with methyl green a prominent nucleus was seen in each cell (Fig. 18).

The reactions of the whole berry and its various parts were next investigated with the following results. The whole berry was digested in distilled water for about twenty-four hours, the temperature being 30°C.; at the end of this time there was found to be a copious yellow precipitate, which on examination under the microscope was found to consist of clumps of spherical masses aggregated together (Fig. 20). The supernatant fluid was poured off from the precipitate, and to it were added two or three drops of Fehling's solution; after warming, a copious brick-red precipitate of cupric oxide was thrown down showing that a glucose was present in the solution, as no precipitate was obtained when the solution was similarly heated without adding Fehling's solution.

The pericarp was stripped off a number of fruits and digested in distilled water for about twenty-four hours, the temperature being about 30°C. The solution was a pale yellow at the beginning, but after digestion the colour was more pronounced and darker, but no precipitate was obtained. Fehling's solution was added to this liquid and warmed, but no precipitate was thrown down. The pericarp was digested in distilled water for twenty-four hours, at a temperature between 60° and 80°C., and at the end of the time a yellow precipitate was obtained, which was found to consist chiefly of clumps of long needle-shaped crystals (Fig. 19); the liquid filtered off from these gave a precipitate with Fehling's solution. Hence the yellow substance contained in the pericarp, which from its micro-chemical and other reactions, solubility

in water, and insolubility in alcohol, chloroform and ether, must be a glucoside, is split up on heating to about 70° C. into glucose and a semi-crystalline substance.

The endocarp, on treatment in the same way as the pericarp, acted in the same manner; on digestion at 30° C. no precipitate was obtained, and the solution gave no glucose reactions; on digestion at a temperature about 70° C. a crystalline precipitate was again thrown down, and the filtrate from this yields a precipitate on warming with Fehling's solution. Thus the substance in the endocarp acts in the same manner as that in the pericarp, both probably being the same glucoside, but contained in much larger quantities in the pericarp. If the seeds be removed and digested for twenty-four hours, at a temperature of 30° C., an opalescent clear solution is obtained; if the seeds are digested at 70° C. the solution still remains clear, showing that the glucoside is not contained in the seed.

The pericarp was digested in water for twenty-four hours with the endocarp; no change took place.

The pericarp was digested in water for twenty-four hours, at a temperature of 30° C., and the solution filtered off, and added to the solution obtained on digesting the seeds for twenty-four hours at 30° C. After leaving them at 30° C. for half-an-hour a precipitate was obtained, which soon became very copious, and which was found to consist chiefly of needle-shaped crystals, and also of the semi-amorphous masses obtained by digesting the whole fruit (Figs. 19 and 20). The filtrate from this precipitate yielded, on warming with Fehling's solution, a copious precipitate. Thus the yellow glucoside has been again split up into glucose and a crystalline substance, and this time not by heat, therefore it must have been by means of some substance contained in the seed.

If the solution obtained from the seeds is boiled for ten minutes and added to a solution of the pericarp, and allowed to stand for twenty-four hours at a temperature of 30° C., no precipitate is obtained, and the solution does not yield a precipitate on warming with Fehling's solution. Hence the

action of the substance contained in the seed which converted the glucoside into glucose and another substance has been destroyed by heat, and consequently that substance is a ferment.

There was thus a ferment in the seed which broke up the glucoside contained in the pericarp and endocarp. I then proceeded to find out in what part of the seed this ferment was contained. The testa was stripped off a number of seeds and digested at the usual temperature for an hour; a clear solution was obtained, which was added to a solution of the pericarp, obtained by digestion as before, and a copious yellow precipitate was obtained in about twenty minutes. The solution obtained from the testa on digestion was boiled for ten minutes and added to the solution of the pericarp; after twenty-four hours no precipitate was obtained. The filtrate in the first instance yielded a precipitate with Fehling's solution, but none was obtained in the second. Hence the ferment, the action of which was destroyed by boiling, appeared to be contained in the testa.

The rest of the seed was taken and digested, and the solution obtained was added to a solution of the pericarp; in about an hour a copious yellow precipitate was obtained, and the filtrate from this precipitate gave glucose-reactions. Hence the ferment, the action of which was also destroyed by boiling in this case, is also contained in the rest of the seed either in the embryo or endosperm, or both.

The embryos of a number of seeds were dissected out and digested as usual, and the solution obtained from them was added to the solution of the pericarp; after a few hours a yellow precipitate was again obtained, the filtrate from which yielded a precipitate on warming with Fehling's solution. Hence the ferment appeared to be contained in the embryo.

The endosperm was removed from a number of seeds and digested for twenty-four hours, at a temperature of 25° C., and to the solution obtained was added the solution obtained by digesting the testa, and the mixture was allowed to stand for twenty-four hours at the same temperature; at the end of the time no precipitate was obtained, and the solution gave no

glucose-reaction, hence the ferment was not contained in the endosperm.

On cutting sections it was noticed that there was a large quantity of a yellow substance in the cells, which however differed considerably from the glucoside of the pericarp in its micro-chemical reactions. In order to see if it was different from the glucoside the embryos of a number of seeds were digested as usual, and to this solution was added a solution of the testa; on allowing to stand for twenty-four hours no precipitate was obtained, and it was therefore concluded that the yellow substance of the embryo was not the same as the glucoside of the pericarp.

Thus in the pericarp there is contained a glucoside, which is split up by a ferment contained somewhere in or near the testa and embryo into glucose and a crystalline substance.

It seemed to be proved from the foregoing observations that the ferment which decomposes the glucoside (xantho-rhamnin), contained in the cells of the pericarp, is localised in the testa of the seed; whether any traces existed in other parts was not proved. On adding water to the intact fruits the soluble ferment passes out and acts on the dissolved glucoside from the pericarp, breaking it up into rhamnin and glucose. If this occurs the precipitate will be withheld chiefly inside the fruits, thus explaining why the dyers should crush their fruits, since it is the insoluble semi-crystalline precipitate which they want.

Before proceeding to show where the ferment really is—in the raphe, a discovery which I only made some time after—it should be stated that the above observations were unavoidably put aside owing to the pressure of new duties. I had, however, made some observations which led to the suspicion that the ferment is even more localised than it had so far been shown to be.

SERIES I.

The following experiments were made with 'Persian berries' —the fruits of *Rhamnus infectorius*—obtained from Kew.

A. Six of the fruits were placed intact in cold distilled water, in a labelled test-tube, and the whole kept at 15° to 16°C. in a hot-house for twenty-four hours, perfectly at rest.

The fruits all floated. In the course of some hours a yellow cloud was observed round the fruits. After twenty hours a copious yellow precipitate had fallen to the bottom of the pale, lemon-coloured liquor: a similar precipitate was sticking to the outsides of the fruits.

B. Six of the fruits were slightly *crushed*, and treated in all respects exactly as in *A*.

The cold water at once turned pale lemon colour, diffusion streaks falling from the floating pieces of fruit as the water dissolved the yellow glucoside from the pericarps: in ten to fifteen minutes the solution was of an intense, clear lemon colour. In two hours a bright golden-yellow precipitate was falling to the bottom, and in three hours there was a copious precipitate[1].

C. Six of the fruits were placed intact in a tube as before, but *boiled* for ten minutes: then treated exactly as in *A*.

A deep golden, clear liquor at once resulted: the fruits fell to the bottom of the tube, leaving the perfectly clear solution above. There was no precipitate—not even a cloudiness—after twenty-four hours.

D. Six fruits were crushed, and then treated exactly as *C*.

The result was the same—no precipitate was formed in twenty-four hours owing to the ferment being destroyed by the boiling.

E. Six of the fruits were dissected, and the outer pericarps alone taken and treated exactly as in *A*.

A pale yellow solution was at once produced, and slowly became more and more intense as the xanthorhamnin was dissolved from the cells. The liquor remained perfectly clear even after twenty-four hours[2].

[1] This precipitate was rhamnin, slowly forming in the quiescent liquor, as the ferment acted on the glucoside, xanthorhamnin: obviously the quicker action here was due to the fruits having been crushed.

[2] And longer, for there was no turbidity to be seen on the following day again.

F. The hard endocarps of the above six fruits (*E*) were taken separately and treated exactly as in *E*.

The endocarps floated, and slowly tinged the water pale yellow[1]. The pale yellow solution remained perfectly clear even after twenty-four hours.

G. The seeds from the above six fruits (there were eleven good large ones) were separately treated with cold water &c., exactly as in *E*.

All floated. The water remained perfectly transparent and colourless even after twenty-four hours. After thirty-six hours I noted a slight turbidity: this increased rapidly, and was found to be due to *Bacteria*.

H. Six fruits were dissected, and the outer pericarps alone taken, and boiled for five minutes in distilled water, then treated exactly as before.

All fell to the bottom, and yielded the same deep clear golden liquor as in *C*. No precipitate or other change resulted, even after fifty hours.

I. The hard endocarps of the above (*H*) six fruits were treated exactly as before, except that they were kept in glycerine (1 vol. glycerine to 1 vol. water). All floated. No change occurred beyond a yellow tinge, as the glycerine dissolved the colouring matter.

K. The twelve best seeds obtained from the six berries dissected (*H*) were placed in a test-tube and glycerine (as in *I*) added. All floated. No change occurred even after fifty hours.

In the next series of experiments, I confirmed more exactly what is already to be seen from a comparison of the above. No precipitate appeared in *C* and *D* because the ferment was destroyed by the boiling: the absence of a precipitate in the case of *E* and *H* is simply due to the absence of the ferment—which exists in *G* and *K*, apart from the fermentable glucoside. *F* and *I* also contain no ferment.

[1] From the layer of cells lining their insides.

SERIES II.

L. I now took the solution *A*, and filtered off the precipitate and fruits from the clear golden liquor.

The liquor contained large quantities of glucose on testing with Fehling's solution. Part of the liquor was allowed to stand, and in twenty-four hours a slight further precipitate had formed. (N.B. This did not occur with the liquor from *C* (q.v.) which had been boiled. Some ferment had no doubt passed through the filter.) The golden semi-amorphous precipitate was then examined microscopically,[1] &c.

M. The contents of test-tube *B* were treated in the same way, and the results were practically the same in all respects.

N. The test-tube *C* was taken, and the clear sherry-gold liquor filtered off from the fruits, and examined. The liquor was divided into three parts, in tubes marked *N*1, *N*2, *N*3.

(1) *N*1. Added a few drops of solution *G* (i.e. cold-water extract of seeds). A copious precipitate of rhamnin was formed during the night.

(2) *N*2. Added a few drops of solution *G*, and *boiled two minutes.* It remained perfectly clear for two days.

(3) *N*3. Added nothing. The solution was perfectly clear next day.

The explanation of this is that the solution of xantho-rhamnin in *C* was incapable of breaking up (*N*3) spontaneously; but is rapidly decomposed when a solution (*N*1) containing the proper ferment is added to it. The action does not take place, however, if the ferment is destroyed by boiling for two minutes (*N*2).

O. I then took the test-tube *D*, and filtered off the clear deep sherry-coloured liquor.

Some was tested for glucose, but gave none. The rest I divided into two parts, in test-tubes marked *O*1 and *O*2 respectively.

[1] The results are embodied in the text.

O 1. To this was added some of the solution *F* (i.e. aqueous extract of endocarps[1]. No precipitate was formed—the solution remained perfectly clear for two days.

O 2. To this were added a few drops of solution *K* (i.e. glycerine extract of seeds). Remained perfectly clear for several hours, but a precipitate fell during the night[2].

P. I then took the test-tube *E*, and filtered the clear yellow liquor off from the pericarps, and divided the solution into three parts, marking the test-tubes *P* 1, *P* 2, *P* 3 respectively.

(1) *P* 1. Added a few drops of the solution *G* (aqueous extract of seeds): an *abundant* precipitate fell during the night.

(2) *P* 2. Added a few drops of solution *I* (glycerine extract of endocarp): no trace of turbidity or precipitate was observable next day—nor after forty hours.

(3) *P* 3. Added a few drops of solution *K* (i.e. glycerine extract of seeds): slight precipitate fell during the night and increased slowly during the following day.

Series III.

I now prepared a series of solutions of different parts of the seeds, each in a labelled test-tube, and placed them in the hot-house for the night.

No. *a*. The testa only of the seeds, with distilled water.

(The liquid remained quite transparent and clear for two days, and then became turbid as *Bacteria* developed.)

No. *b*. The testa only used, and pure glycerine poured on it.

A perfectly clear, colourless solution resulted.

No. *c*. Endosperm and embryo cleaned of testa, taken and extracted with cold distilled water.

A limpid colourless extract resulted. (Traces of turbidity next day, and after forty-eight hours it was dirty-white and cloudy[3].)

[1] I only repeated this experiment here to make the series more complete: no trace of the ferment occurs in the endocarp.

[2] The precipitate formed much more slowly than when the aqueous extract of the seeds were used.

[3] Bacteria, &c.

No. *d*. Endosperm and embryo—as clean as possible, but cannot be sure of their purity.

(In two days turbid and dirty-white from Bacteria, &c.)

No. *e*. A few drops of No. *a* (i. e. aqueous extract of testa) were added to the clear solution *H* (i. e. boiled aqueous extract of pericarps).

The No. *a* solution had been prepared 1½ hours; the *H* solution two days; the transparent yellow solution yielded a dense yellow precipitate during the next hour. Other portions of *H* remained clear for two days [1].

No. *f*. To another sample of the yellow solution *H*, I added a few drops of No. *c* (i. e. aqueous extract of clean endosperm, 1½ hours old).

No precipitate was formed.

No. *g*. Another sample of *H* was allowed to stand for forty-eight hours.

No precipitate formed.

The following series of experiments were made with parts of seeds which had been kept dry for two years:—

SERIES IV.

No. 1. Glycerine (pure) extract of embryos only.

Slowly formed a yellow clear solution which remained clear for days.

No. 2. Aqueous extract of embryos only.

At once formed a yellowish solution. It remained clear for twenty-four hours, but flocculent clouds appeared in two days [2].

No. 3. Aqueous extract of the thickened inturned margins of the seed.

At the time I thought this consisted of the testa only, but pieces of the raphe were also attached.

[1] This apparently again shows that the ferment is in the testa; but see below.

[2] Bacteria.

A slightly opalescent colourless solution. Turbid in two days.

No. 4. Aqueous extract of endosperm, cleared from embryo and testa.

A colourless solution; slightly opalescent in two days.

No. 5. Aqueous extract of pieces of testa taken from the *sides* of the seed.

(The testa can be more easily removed *clean* from the sides of the seed than elsewhere.)

Clear colourless solution.

No. 6. To a fresh solution of boiled pericarps, prepared and filtered as before, I added a few drops of solution No. 1 (i. e. glycerine extract of embryos) which had stood for 1½ hours in hot-house.

No results in two days.

No. 7. To another portion of the pericarp extract added a few drops of solution No. 2 (i. e. aqueous extract of embryos), same age, &c.

No results in two days.

No. 8. To a third portion of pericarp extract added a few drops of solution No. 3 (i. e. aqueous extract of thick margins of testa—and raphe, as I discovered later).

A dense yellow precipitate began to fall in half an hour, and became more and more abundant during the night.

No. 9. To a fourth portion of extract of pericarp added a few drops of solution No. 4 (i. e. extract of endosperm in water): same conditions.

No results at all.

No. 10. To a fifth portion of the same pericarp extract added a few drops of solution No. 5 (i. e. aqueous extract of *sides* of testa only).

Next day were very doubtful traces of turbidity, but not the slightest precipitate [1].

[1] Nor did any precipitate fall in the next twenty-four hours.

No. 11. To a sixth portion of the pericarp solution added nothing.

It remained unaltered and clear for two days.

It had now become clear that (1) the ferment is contained somewhere in the seed; (2) it is confined broadly to the testa or outer coat of the seed; and (3) moreover is localised—situated somewhere in *or near* the thickened margins where the testa is turned in. (4) The ferment is not destroyed by keeping for two years.

I now repeated many of the experiments given above, with the seeds and fruits of the same species (*Rhamnus infectorius*) but from another source, and which had not been kept so long. I first dissected twenty-four seeds, under the simple microscope, separating the thickened margins of the testa (where it is turned in) from the rest of the seeds—i. e. the testa of the sides, the endosperm, and the embryos.

Series V.

γ. An aqueous extract of the thickened inturned margins of twelve seeds.

Yielded a perfectly clear colourless liquid.

δ. Aqueous solution of the rest of the twelve seeds (i. e. the endosperm, embryos, and the testa from the sides of the seeds).

Yielded a clear, colourless liquid[1].

η. A glycerine extract of the thick inturned margins only of twelve seeds.

Perfectly clear extract.

θ. A glycerine extract of the rest of the seeds.

Clear solution.

I then added a few drops of each of these extracts to a series of test-tubes containing fresh boiled solutions of the glucoside (xanthorhamnin) obtained from the pericarps.

[1] Faint tinge of yellow.

The tubes were labelled, and treated as before. We may call this

SERIES VI.

A*. A few drops of the extract γ (i. e. aqueous extract of margins of testa) added.

A dense cloud formed in ten minutes, and an abundant golden precipitate was falling in fifteen minutes.

(N.B. All the following tubes were still perfectly clear.)

B*. A few drops of solution δ were added (this was an extract of all the rest of the seed).

A precipitate was *slowly* forming three hours later: this slowly increased, and was abundant next day[1].

C*. A few drops of solution η (i. e. glycerine extract of thick margins only) were added.

A slight precipitate had fallen in two hours, and increased soon after till it was as copious as in A*.

D*. A few drops of θ were added (i. e. glycerine extract of all the rest of the seed).

This remained perfectly clear for many hours, but a precipitate fell next day.

Here was an apparent contradiction of some of my previous statements and conclusions, and it became necessary to see why the precipitate fell in the tubes containing the extracts of other parts of the seeds than the thick margins. Before explaining this, however, I will give one more series of experiments.

SERIES VII.

E*. To a fresh solution from boiled pericarps added the thickened inturned margins of six seeds, dissected away as clean as possible under the simple microscope.

A precipitate began to form after three hours, and this was abundant next day.

[1] I shall show below that this was contaminated, and how.

F*. To another portion of the pericarp solution I added the cleaned sides of the testa only of the same six seeds.

The solution remained clear for two days.

G*. To another portion of the pericarp solution added the dissected out endosperm and embryos from the six seeds.

The solution remained perfectly clear for two days.

H*. Another portion was allowed to stand untouched, and it remained clear for several days.

Here then we see that no ferment was present in the *sides of the testa*, the endosperm, or the embryos: how was it, then, that the ferment existed in the solutions B* and D* of Series VI? This question is best answered after examining Fig. 21. It will be noticed that the raphe (adherent funicle) of the seed runs in the dorsal depression of the seed, and that *it is adherent to the testa proper* all along the sides of the groove of the seed. In other words, when the testa begins to harden, the lignification does not extend to the raphe, but is confined to a layer of cells—the outer integument of the ovule—which runs inside the raphe. When the fruit and seeds are dried, the thin-walled parenchyma of the raphe shrivels up, and it is not very easy to detect it when dissecting the seed, unless its presence has first been pointed out. As shown in Figs. 21 and 22, however, this raphe is organically continuous with the testa at the groove, and it is almost impossible to clear it away from the hard testa at this part. As soon as I had got at the fact that it is the *raphe* which contains the ferment (and this follows with certainty from the experiments below) all the errors were cleared up. First, however, I had perhaps better give the results.

It had struck me several times that the ferment was very energetic, because such a mere trace of the solution containing it caused such copious precipitates to form. This being the case, I prepared a series of moist chambers, such as are used for growing Fungi, &c. in beneath the microscope. I then cut fairly thin transverse sections across the whole seed—dry and unaltered—as shown in Figs. 2, 3, 21. It was now very

easy to separate very tiny bits of the various parts, testa, endosperm, embryos, and *raphe*. I then did this with needles. I first separated a minute piece of the raphe, and placed it in a tiny drop of fresh extract of pericarps, hanging from the cover slip over the moist cell: then I heated the needle points and separated a bit of the outside testa, and placed it in a similar hanging drop; and so on with endosperm and embryo.

The result was startling. A copious precipitate had formed in the drop containing the bit of raphe, before I had finished preparing a second specimen—i.e. in less than five minutes. Summing up the results of numerous repetitions of these experiments in drops, I find that the slightest piece of the raphe causes decomposition of the glucoside xanthorhamnin in two or three minutes: under the microscope a cloud of minute black dots (black because so small?) arise in the previously clear yellow solution, and grow under the eye of the observer into the typical semi-crystalline yellow masses of rhamnetin. The whole process occupies a few minutes, and I have now demonstrated it several times to others.

We now see why some of my previous experiments yielded ambiguous results. Starting from the fact that the slightest trace of the ferment—and therefore the merest little piece of raphe containing it—will start the decomposition, it is easily seen that while bits of the thickened margins of the inturned testa (which always have adherent to them cells of the raphe) produced the decomposition, the pieces of outside testa from other parts of the seed could easily be got clean, and no decomposition followed. In cases where I neglected the presence of the shrivelled film of raphe adhering to the testa lining the groove, as in No. 8 (Series IV), B* (Series VI), D* (Series VI), there were portions of the raphe adhering to some of the pieces dissected out, hence the apparently contradictory results.

As a final illustration of the power of the ferment, I may quote the following experiment. I prepared five cubic centimetres of the solution from the pericarp, and placed the raphe (carefully separated) of *one* seed in it: the raphe floated,

partly because it had air clinging to its dry cells. In ten minutes the floating raphe was thickly covered with the golden yellow precipitate of rhamnetin. In twenty minutes the clouds of precipitate were falling in the tube: in less than an hour there was a precipitate at the bottom of the test-tube, which measured $1\frac{1}{2}$ mm. in depth, and which was many times larger than the raphe.

Examination of the raphe shows that it consists of a slender vascular bundle running up the groove in the seed, which is dorsal, and cellular prolongations like wings from its sides: these two wing-like expansions of thin-walled parenchymatous cells line closely the sides of the groove (Fig. 21). In fact we may regard the vascular bundle of the raphe as the line round which the folding occurs which gives the seed its grooved appearance, and therefore its horseshoe-shaped transverse section. When the folding of the seed occurs, it doubles back with it the two wings of the raphe, and the margins of these wings end in the thickened ridges of the testa, as shown in the figures.

I also examined the contents of the cells of the raphe. When a thin section of the dry raphe is placed in strong glycerine the cells are seen to contain a brilliant, oily-looking, colourless substance which does not fill up the cavity but is driven aside by large vacuole-like chambers in which a few brilliant granules may be observed. If placed in very dilute solutions of caustic potash, the cells and their contents at once swell up, and the oily-looking matrix dissolves almost entirely, but not quite; drops of clear oil-like substance flow together, and escape.

When placed directly in water, the colourless oil-like matrix froths up in a most remarkable manner, and oily-looking drops escape; these drops are vacuolated, however, and something seems to be dissolved from them also. In one per cent. Osmic acid solution, the vacuolated oily masses slowly turn brown. Absolute alcohol dissolves a large proportion of their substance, but not all.

I have examined the fruits and seeds of four other species

of *Rhamnus*—viz. *R. tinctorius*, W. & K., *R. Carolinianus*, Walter, *R. Wicklius*, and *R. catharticus*, L.—but have found no trace of the ferment in any of them. This being the case, I shall sum up the chief points respecting these fruits, &c. in a very few words.

All the fruits were ripe, and the pericarps dark purple and soft, yielding violet and purple brown solutions when extracted with water. The colours of the solutions soon change and become browner or redder, and paler. The addition of a few drops of ammonia in all cases turns the purple or brown solutions green, apparently due to the formation of a pigment like 'sap-green.' These brown or purple solutions also contain glucose, precipitating abundantly from Fehling's solution.

In no case was I able to obtain any ferment action when the seeds of any species were added to the extract from the pericarps of its own or other fruits. The seeds did not precipitate rhamnetin in the solutions of xanthorhamnin obtained from the pericarps of *Rhamnus infectorius;* nor did the seeds of the latter species cause any precipitate to form in the liquors obtained from the pericarps of the above four species. It seems safe to conclude, therefore, that no ferment is present in the seeds of these four species, at any rate when the fruits are ripe.

This raises the question, is the ferment present in the seeds of *R. infectorius* when fully ripe? I cannot yet answer this question, because I do not know whether the fruits used in the trade as 'Persian Berries' are ripe when gathered. Probably they are not, but are cured while yet not quite mature.

If the precipitate of rhamnin is chiefly withheld inside the fruits, this explains why the dyers obtain poorer results by this method, since the crystalline precipitate of rhamnin is what they want.

The soluble ferment was regarded as probably existing in well-protected sclerenchymatous but pitted cells of the testa, as a fine granulated mass; but I have now demonstrated that it exists in the parenchymatous cells of the raphe.

We have now to enquire as to the biological significance of these matters. I have germinated the seeds of *Rhamnus infectorius* once or twice, but have frequently failed to make the seedlings grow at all.

So far it has been only from whole fruits that seedlings were obtained: all the specimens of shelled naked seeds have failed. In the successful cases the pericarps swell, and become yellow and slimy, the soil around being dyed with the colouring matter, and fungi seem particularly apt to appear on the rotting pericarps. It seems an obvious suggestion that this is due to the glucose. But it is also a suggestion worth further investigation that the glucose is of use to the young embryo, and I am strongly inclined to the belief that this is the case, and that the cause of failure with naked seeds lies partly in this. At the same time the matter needs further investigation.

Another point is--do birds or other animals eat the fruits? I find them distinctly bitter and resinous to the taste at first, and they are known to be purgative. It seems not unlikely then that they are not eaten by animals, though they may be carried and broken by them.

My idea that the glucoside stored in the pericarp is for the benefit of the young plant is not without support from analogy, and it is well known that the amygdalin of bitter almonds is contained in certain cells of the seed, the ferment (emulsin) in other cells: so also with mustard seeds—the ferment (myrosin) which breaks up potassium myronate into glucose and other bodies exists apart in the seed.

It is, however, a peculiarity that in this case the glucoside should be in the pericarp and the ferment in the raphe of the seed, a phenomenon which is again suggestive in view of our growing conviction that many glucosides, hitherto regarded as more or less waste products, are really not excluded from the constructive metabolism of the plant.

EXPLANATION OF FIGURES IN PLATES I. & II.

1. Whole fruit of *Rhamnus infectorius*. *a* with three seeds. *b* with four seeds.

2. Transverse section across the whole dried fruit. *p.* pericarp. *enp.* endocarp. *t.* testa. *enm.* endosperm. *em.* embryo.

3. Transverse section of one seed. *t.* testa. *enm.* endosperm. *em.* embryo.

4. Transverse section of part of the seed in water. *t.* testa. *enm.* endosperm. *cot.* cotyledons. Between the testa and endosperm a layer of broken down cells. Zeiss D/$_2$ reduced one half.

5. Transverse section of the pericarp, examined in water. Zeiss D/$_2$.

6. Transverse section of the pericarp, examined fresh in glycerine. The yellow substance (*a*) in the cells is already dissolving. D/$_2$.

7. Transverse section of endocarp, examined in glycerine. Typical sclerenchymatous cells, with the lumina nearly obliterated. F/$_2$.

8. Inner surface of the endocarp shaved off, examined fresh in glycerine. The yellow substance in the cells already partially dissolved. D/$_2$.

9. Inner surface of the endocarp, after being left some time in glycerine. The yellow substance has completely dissolved. D/$_2$.

10. Transverse section of the inner layer of the endocarp, the cells seen in (8) and (9). D/$_2$.

11. Very thin transverse section of the testa in glycerine. Hard sclerenchymatous cells, with a number of pits in the walls. D/$_2$ reduced one half.

12. Tangential section of the testa in glycerine, showing sclerenchymatous cells with pitted walls and containing a granular substance of greyish colour. D/$_2$.

13. Tangential section of endosperm in glycerine, containing fat and aleurone. D/$_2$.

14. Tangential section of endosperm, in glycerine after water and after the fat has been dissolved out in absolute alcohol. D/$_2$.

15. Tangential section of endosperm, which had remained 72 hours in a 2 % solution of mercuric chloride in absolute alcohol, washed ½ minute in water, stained with eosin, and mounted in potassium acetate. The cells contain aleurone in which no enclosure could be detected. The aleurone dissolved in water. F/$_2$.

16. Tangential section of endosperm, 24 hours in the mercuric chloride solution, ½ minute in absolute alcohol, 5 minutes in eosin, and 1 minute in water, mounted in potassium acetate. The aleurone is dissolved out, leaving holes in the matrix, and the nucleus is stained. F/$_2$.

17. Transverse section of one of the cotyledons in glycerine, after removing the fat with absolute alcohol. *f.v.b.* vascular bundle. D/$_2$.

18. Tangential section of a cotyledon in glycerine. *f.v.b.* vascular bundle.

19. Crystalline precipitate, obtained on adding the solution obtained from the pericarp to the solution obtained from the seeds. D/$_2$.

20. Amorphous precipitate obtained on digesting the whole berry. D/$_2$.

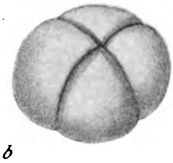
21. Transverse section across the middle of a seed, at a level higher than that of Fig. 3. *t.* testa. *enm.* endosperm. *cot.* cotyledons. *r.* funicle (raphe). *m.* thickened margin or ridge of testa. *f.v.b.* vascular bundle of raphe.

22. More highly magnified view of the part of Fig. 21 enclosed in the square. *to.* outer testa. *ti.* inner testa. Other lettering as in Fig. 21.

23. Cells of the raphe in which the ferment is contained.

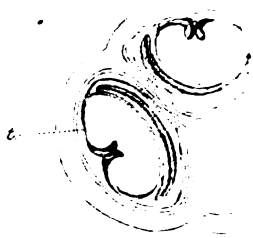
Fig. 1.

a



b

Fig. 2.



c

Fig. 5.

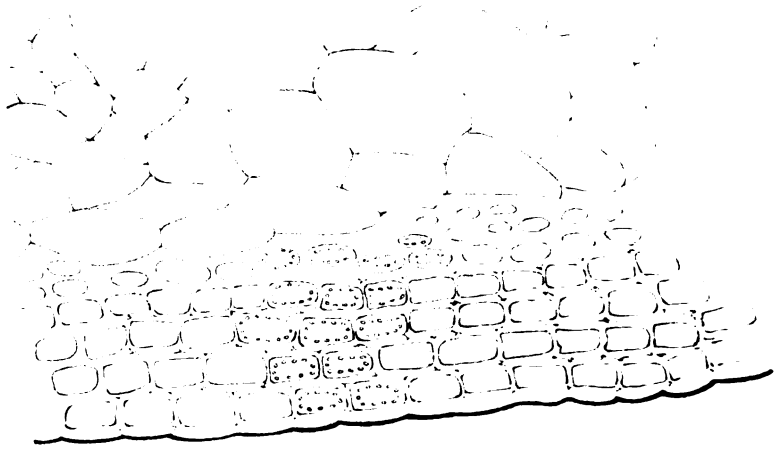


Fig. 7.

Fig. 8.

Fig. 3.

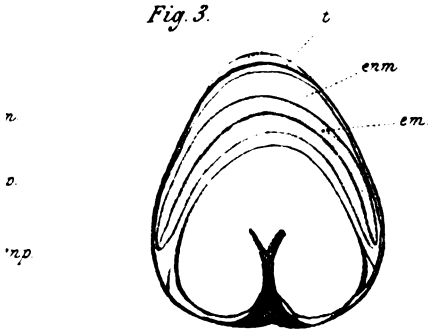


Fig. 4.

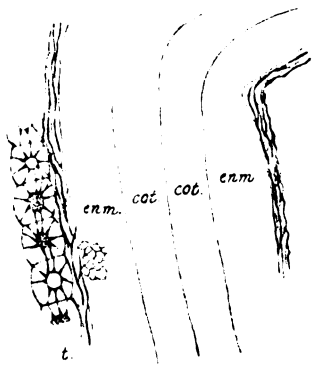


Fig. 6.

g. 9.

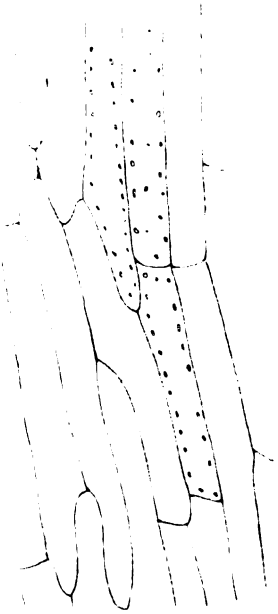


Fig. 10.

Fig. 11.

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Fig. 12.

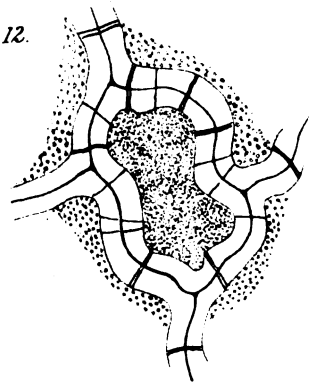


Fig. 13.

Fig. 16.

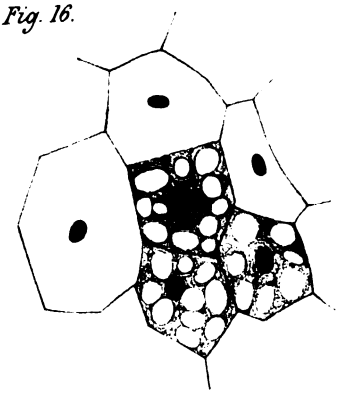


Fig. 17.

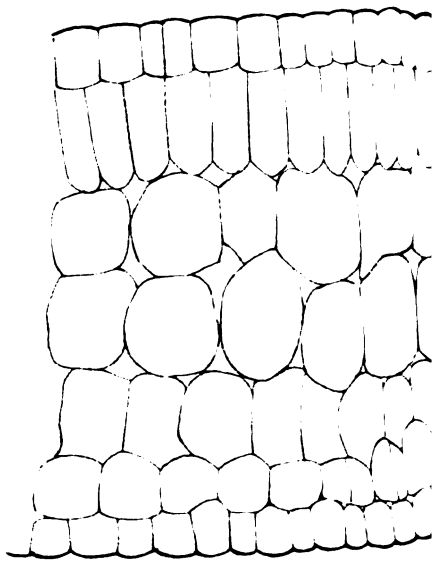
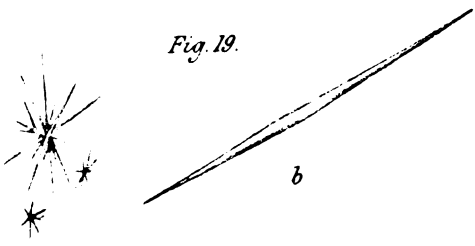


Fig. 20.

Fig. 19.



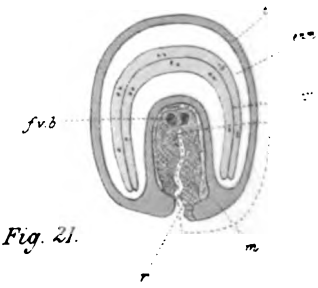


Fig. 21.

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14.

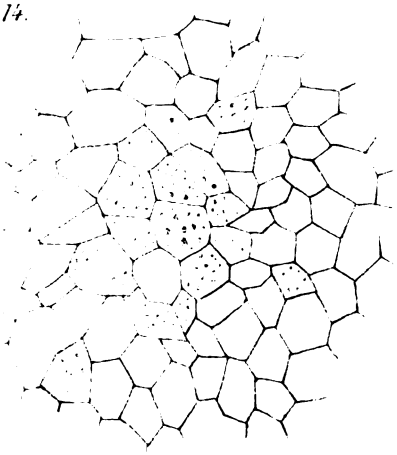

Fig. 15.

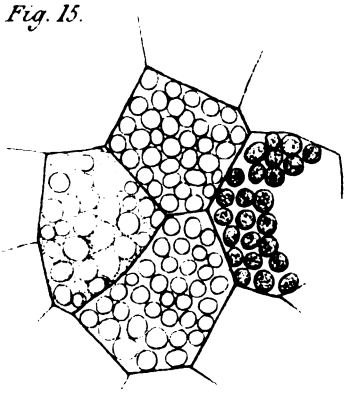

Fig. 18.

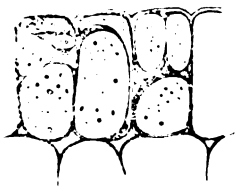

Fig. 23.

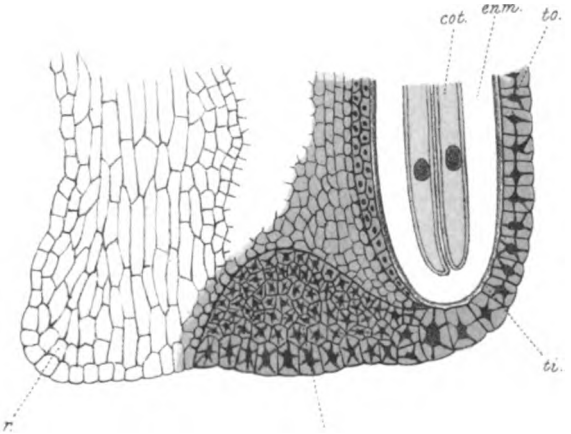

Fig. 22.

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On the structure of the mucilage-secreting cells of Blechnum occidentale, L., and Osmunda regalis, L.

BY

WALTER GARDINER, M.A.

AND

TOKUTARO ITO, F.L.S.

With Plates III and IV.

I. INTRODUCTORY AND HISTORICAL[1].

IN ascending the Vegetable Kingdom it is among the Ferns that we first meet with any great variety in the forms of the hairs which occur on the young, or the adult, stem and leaf. At this point, however, associated with a rapidly increasing complexity of the aerial members, we find trichomes of the most diverse structure and function which may even rank with those of the highest of the Dicotyledons, and among the most interesting are the hairs which are endowed with the power of secretion, and thus contribute in an especially marked manner to some physiological necessity of the plant upon which they are borne.

Such hairs have been long known. From the point of view of their secretion they may conveniently be divided into two classes, namely those secreting mucilage and those secreting

[1] In the case of composite papers it is not uncommon to attach all the credit to the person whose name appears first upon the title-page. I wish distinctly to state that it must not be so in the present instance. The work was certainly suggested by myself and carried out under my direction, but we have each of us done our own share in the investigation and worked in common through all the results. To Mr. Ito indeed fell the task, not only of making observations, but also of drawing the whole of the figures, and their wonderful and appreciative realism will sufficiently prove his capabilities more than any remarks of mine can do. For writing the paper I am myself responsible.—WALTER GARDINER.

[Annals of Botany, Vol. I. No. I. August 1887.]

resin. The capitate mucilage-secreting hairs, which have been since shown to occur very commonly on the young stems, leaves and paleae of so many ferns, were first figured in the case of *Polypodium aureum*, L., by Suminski[1] in his excellent and well-known drawings of young germinating plants. Hofmeister[2] represents similar hairs of *Pteris aquilina*, L., and those of the young scale (palea) of *Polypodium serpens*, Forst, and Kny[3], in the case of *Ceratopteris thalictroides*, Brongn., figures the various stages in a developing scale in all of which the terminal mucilage-secreting hair is well shown. Hitherto but little notice had been taken of the more minute histology of the structures; and it was Prantl[4], and after him Sadebeck[5], who described the mucilaginous character of the cell-contents. In the case of *Osmunda regalis*, L., de Bary[6] drew attention to the long septate mucilage-secreting hairs; and quite recently Goebeler[7], in his paper 'Die Schutzvorrichtungen am Stammscheitel der Farne,' gives by far the most complete account extant, not only of the general distribution of secretory and protective hairs throughout the Filicineae, but also of their histology and physiological significance.

We may now pass on to the literature of the resin-secreting glands, and here the unique intercellular hairs of *Aspidium Filix-mas*, Sw., claim the first place. These occur in the intercellular spaces of the rhizome and the base of the petiole, and as Sachs[8] afterwards showed in a similar position in the leaf-parenchyma. They were observed by Mettenius[9], but to

[1] Suminski, Zur Entwicklungsgeschichte des Farnkraüter, 1848.

[2] Hofmeister, Vergleichende Untersuchungen, Leipzig, 1851, and in Abh. d. König. Säch. Ges. d. Wiss., 1857.

[3] Kny, Entwick. d. Parkeriaceen, 1875.

[4] Prantl, Morphologie d. Gefässkryptogamen, 1881.

[5] Sadebeck, in Verhandlung d. bot. Ver. d. prov. Brandenburg, 1884. He figures young mucilage glands of *Asplenium Serpentini*.

[6] De Bary, Comparative Anatomy of Phanerogams and Ferns, p. 99. The hairs were first described by Milde, Monogr. generis Osmundæ, Vindob. 1868.

[7] Goebeler in Flora, 1886.

[8] Sachs, Textbook of Botany, 2nd ed. p. 439. Sachs also figures the mucilage-glands of the sporangia of *Aspidium Filix-mas*.

[9] Mettenius, Filices horti Lipsiensis, Leipzig, 1856.

Schacht[1] belongs the credit of bringing these remarkable structures more prominently into view by describing and figuring them in his paper in Pringsheim's Jahrbuch. Besides the intercellular hairs other resin-secreting trichomes of similar structure occur on the paleae of various species of *Aspidium*. Thus de Bary[2] mentions *Aspidium Filix-mas*, Sw., *Aspidium spinulosum*, Sw., and *Aspidium molle*, Sw., as possessing capitate glandular hairs, and Goebeler[3] shows that in *Aspidium Sieboldi*, Van Houtt, like glands occur. We may also add to the list *Blechnum occidentale*, which bears resin-glands both on the paleae and the young leaves. Any account of the secreting hairs of ferns would obviously be incomplete did we not allude to the resin-glands which characterise such ferns as the species of *Gymnogramme*. They are of course quite homologous to those already described, except that the secretion appears in the form of numerous rods which stand out on all sides upon the surface of the secreting cell. The substance secreted appears to be partly resinous and partly waxy in character. They are fully described by de Bary[4] who gives the literature connected with them, and Goebeler also briefly alludes to them in the exhaustive paper to which we have already referred. Hairs of the *Gymnogramme*-type, producing their dusty-looking secretion in the form of resin-rods, persist even on the adult leaves, but the glandular hairs which we now describe are associated distinctly with bud-formations; they are therefore transitory in character. Whether on the leaves or paleae, they can only be observed in the youngest members, and here their secretory character is very marked, the whole apical portion of the young shoot being usually bathed with the mucilage derived from them. The hairs are very simple in structure, consisting either of a filament of cells all of which secrete (*Osmunda*), or occurring as stalked capitate hairs (*Blechnum*) when only the end cell is glandular. In the same individual both resinous and mucilaginous hairs may occur, but the first development of the two forms is quite similar,

[1] Schacht in Pringsheim's Jahrb., Bd. III.
[2] De Bary, loc. cit., p. 89.
[3] Goebeler, loc. cit.
[4] De Bary, loc. cit., p. 99.

and the most important difference between them consists in the kind and manner of secretion. The physiological function of these glandular structures has already been sufficiently treated by Goebeler. One would here briefly point out that the mucilage and resin serve a most important purpose in the plant-economy, particularly by preventing too excessive transpiration in the young and delicate buds, and by serving as a reservoir for water against times of drought. Similarly the woolly hairs protect the plant both from injury from without and from the dangerous effects of extreme variations of temperature.

In the present paper we attempt to give a more detailed account than has hitherto appeared of the minute histology of two forms of mucilage-secreting hairs, viz. those of *Blechnum occidentale*, L., and *Osmunda regalis*, L., and we also endeavour to describe the various phenomena which are associated with mucilaginous secretion. This work was suggested partly by Prof. de Bary's remarks upon the mucilage-hairs of *Osmunda regalis*, L.[1], and partly by an observation made by the first-mentioned of the present authors, that in *Blechnum brasiliense*, Desv., there were mucilaginous hairs associated with the young bud.

II. Method of Research.

The observation of the secretory structures of which we write presents but little difficulty. All but the very youngest leaves having been removed from the fern-shoot under examination, the developing paleae or the developing leaves are separated as required, and then further dissected and teased out under a low power of the dissecting microscope. By this means hairs of all ages may easily be obtained.

Fresh material gives by far the most satisfactory results. Alcohol causes abnormal shrinking of the mucilage attended by great distortion of structure. Saturated watery picric acid on the other hand produces great swelling of the mucilaginous contents, which finally ends in the rupture of the cell and the

[1] De Bary, loc. cit., p. 99.

escape of the mucilage contained in them. Chromic acid is more satisfactory. A solution of 1·5 to 2·0 per cent. strength was employed and the tissue was exposed to its action for twenty-four hours and was then freely washed in water. By the use of so strong a solution the voluminous tannin-precipitate which first appears is subsequently dissolved in the excess of the reagent, and after washing the cell appears clear and the tannin has been removed[1]. The observation of fresh material mounted in iodine or in ·5 to 1 per cent. of osmic acid gives excellent results[2]. With iodine the deeply stained brown protoplasm and nucleus are sharply contrasted with the clear yellow mucilage, and with osmic acid the mucilage-drops which contain tannin stand out dark and well defined, while the ectoplasm and the endoplasmic framework remain hyaline and brilliant with just the faintest yellow coloration. With both these reagents the cell-contents are exceedingly well preserved.

Picronigrocin (24 hours) was also employed with success, and such material, after washing in water and mounting in glycerine, furnished quite the most satisfactory permanent preparations. As staining reagents, iodine, osmic acid, Hanstein's violet-fuchsin, haematoxylin, methylene-blue, Hofmann's blue, and eosin were chiefly used. Both Hanstein's violet-fuchsin and eosin were especially valuable, not only on account of their staining properties, but also for the comparative rapidity with which they diffused into the cell contents; with these exceptions, the aniline dyes penetrated the mucilage with great difficulty, and long and patient treatment, with repeated observation, was required. In the various details of washing, and during micro-chemical investigation, the well-known refractory properties of mucilage were only too well marked, rendering much of the necessary manipulation both trying and tedious.

[1] This method was first used for the tentacles of *Drosera*. See Gardiner in Proc. Roy. Soc. 240 (1886).

[2] This applies to *Blechnum* only. The hairs of *Osmunda* contain such an enormous quantity of tannin that the whole of the tincture is blackened.

III. Special Observations.

(a.) Blechnum occidentale, L.

This species was used in preference to *Blechnum brasiliense*, Desv., both because it demonstrated more clearly the minute histology of the gland-cells, and also on account of its freely branching habit which ensures the production of a sufficient supply of growing points. The stem is provided with numerous paleae, and both on the structure and on the young leaves there are numerous mucilage and resin-secreting gland-cells (Figs. 1, 2, and 3). In each of the paleae the apex is terminated by a single mucilage-gland borne on a long stalk which is filamentous and multicellular. This stalked gland is developed at a very early stage in the history of the scale (Fig. 4), and by the time the rest of the glands are produced along the scale-edge, and have become functional, the apical cell has perished and its contents have usually quite disappeared (Fig. 1). With the exception of this terminal cell which always secretes mucilage, the remaining glands may be either entirely mucilaginous or entirely resinous in character, or in many cases both forms may occur. The resin-glands are usually simple and sessile, and the secretion appears outside the cell-wall, collecting beneath the cuticle which becomes raised up like a blister, as in so many resin and oil-producing hairs (Fig. 31). The mucilage-glands are usually stalked and the secreting cell is large and swollen, but the secretion escapes in this case only on the rupture of the cell-membrane (Fig. 27). The foregoing remarks upon the anatomy of the paleae-hairs will equally apply to those of the leaves. Both mucilage and resin-glands occur distributed over the surface. The mucilage-hairs are especially localised in relation to the vascular bundles, and rows of them arise from those epidermal cells which are placed immediately above the main vascular trunks. In like manner the resin-hairs are met with in greatest number along the edge of the young leaves. Having teased out and mounted a preparation

of young paleae and leaves, the attention of the observer is soon drawn towards the large swollen mucilage-cells. They may be seen in various stages of development, and perhaps the more usual and typical forms are those represented by Figs. 5, 6 and 7.

The glands of the paleae are more conspicuous than those of the leaf on account of their greater size and the more highly refractive character of the mucilage secreted by them. The latter substance occurs in the younger glands as a number of brightly shining isolated drops (Fig. 5), which soon appear to lose their distinct outline and to become clubbed together into a single irregular and lobular mass (Fig. 6). Later on, the entire cell appears to be filled with the mucilaginous secretion, which is highly refractive and contains a number of darker granules disseminated throughout its substance (Fig. 9). In other gland-cells the mucilage appears to be differentiated into an inner and granular central mass surrounded by a broad and hyaline outer layer (Figs. 7 and 8), and here almost any one would suppose that at any rate a portion of the mucilage arises from the degeneration of the inner layers of the cell-wall. Lastly, careful observation will usually demonstrate that in the isolated drops which are shown so well in the younger gland-cells, numerous minute droplets are present which may moreover be recognised in the older glands also (Figs. 10, 11, 12 and 8). The protoplasm is in all cases clear and difficult to define.

We may at once remark that in reality all the mucilage is secreted by the protoplasm, and that in the very oldest cells remains of the ectoplasm and of the nucleus can be shown to be present outside the mucilage-mass. The very transparent character of the protoplasm causes the satisfactory demonstration of this fact to be often a matter of some difficulty, and we found this to be especially the case in our investigations concerning the origin and development of the mucilaginous drops. Again and again, from every standpoint we have returned to this question, and after numberless observations we feel that we have established beyond all doubt that the whole of the

mucilaginous secretion is entirely intra-protoplasmic, and that the cell-wall takes no part whatever in the phenomenon.

The earliest stage of development of the secretory hairs is indicated by the arising of a papillose outgrowth from one of the ordinary epidermal cells. This may be a cell occupying any position in the case of a young leaf, but in the paleae it must be one which is situated along the edge of that structure. The papilliform protrusion is soon cut off by a transverse wall and may then again divide once or several times (Fig. 14). It is always the apical or head-cell which exhibits the secretory function. All the cells both of the leaves and paleae possess large and distinct nuclei, and numerous plastids are also present. No movement of the protoplasm of the stalk-cells could be detected as in the case of *Ononis spinosa*, L.[1] Even more markedly than the rest, the young gland-cell exhibits the well-defined nucleus and plastids of which we have spoken, and here the commencing vacuolation and the delicate strands of protoplasm, stretching on all sides from the nucleus to the peripheral lining of the cell-wall, appear to exquisite advantage and beauty (Fig. 15). As the cell grows the usual single vacuole is formed and the protoplasm takes up its well-known position, lining the rapidly enlarging cell-membrane as a delicate primordial utricle. Both the nucleus and the plastids are then found to be situated on the inner side of the ectoplasm as in *Chara*[2]. The secretory change first begins in the endoplasm, commencing just beneath its free surface and simultaneously over the entire area which immediately bounds the cell-vacuole (Fig. 16). It then spreads into deeper and deeper layers until the whole of the endoplasm takes part in the process. After some time the plastids are gravely affected by the various changes which are taking place, and they eventually become disorganised, and disappear, yielding up their own substance to contribute to that of the secretion. In the nucleus also, great degeneration occurs, and at the period of rupture of the

[1] Behrens in Ber. deutsch. bot. Gesellschaft, Bd. iv. (1886), p. 402.

[2] Sachs's Textbook of Botany, 2nd Engl. ed., p. 304.

cell-wall and escape of the secretion the ectoplasm and the disorganised nucleus are the only structures which still remain in connection with the cell-membrane, the dead and equally disorganised endoplasmic framework escaping with the mucilage (Figs. 9 and 27).

Tannin can be demonstrated in quite young cells, and from this point onwards it steadily increases in amount, although it never occurs in such great quantity as in *Osmunda*. With the exception of its transverse basal wall the cell-membrane undergoes cuticularisation over the whole of its surface, but it is only the more external of the wall-lamellae that are thus affected. The inner layers retain for some time their primitive cellulose character, but at length they suffer hydration and become converted into a substance of a mucilaginous nature. This latter, although it undergoes but little swelling, is capable of great extension, as the very large size of the bladder-like glands sufficiently proves. The transverse basal wall, which separates the head from the contiguous stalk-cell, is much more pronouncedly mucilaginous, and gives a well-marked pink colour with corallin-soda.

We are now in a position to describe in detail the various phenomena connected with mucilaginous secretion. We have already stated that this substance is directly derived from the protoplasm, and we may further add, that the various changes which give rise to its formation are undoubtedly of a katabolic nature. In all the cases which we have investigated the mucilage arises in the form of small drops, all of which grow to a fixed definite size, and the number of the drops is continually increased by repeated basipetal formations until the energy of the protoplasm is exhausted and the gland-cell is full (Figs. 16 and 17). The first few drops appear to burst into the vacuole, causing it to assume a certain mucilaginous character, but, apart from this exceptional phenomenon, all the various drops remain distinct, each being completely shut off from its neighbour by its own portion of the delicate protoplasmic reticulum which constitutes a framework for the whole system of drops in the secretory cell.

The successful observation of the developing drops was found to be one of the most difficult points connected with the present research, but by the use of osmic acid we were at length able to set the matter at rest, and subsequently also to observe the same phenomenon in fresh glands. As our figure (Fig. 16) shows, the development commences at a very early period. Our drawing was taken from a hair which had been treated with a 1 per cent. solution of osmic acid. The mucilaginous contents of the vacuole are contracted by the action of the reagent, leaving a portion of the lining protoplasmic membrane and of the threads going to the nucleus clear and free. At various points here and there numerous small bubble-like utricles may be seen, and these represent the young developing mucilage-drops. The secretion arises, as we have already stated, just below the surface of the endoplasm, and the drop, enclosed by its delicate protoplasmic membrane, protrudes into the cell cavity. Having reached a definite size, its growth ceases and a new drop soon commences to form just below, and thus by repeated basipetal formations immediately beneath the various drops contained in the cell, the latter becomes after a time quite filled by them and even the vacuole-space is entirely eliminated. Fig. 17 shows in a very clear manner the formation which we have described. In the adult cell the protoplasm appears as a delicate reticulum containing the various drops in its meshes, the whole system being bounded by the ectoplasm and contained within the cell-membrane (Figs. 11 and 19). All the protoplasm is for some time living and functional, but in course of time it experiences degeneration-changes, and ultimately death ensues, commencing in the more central protoplasm and gradually spreading to that at the periphery. The remains of the disorganised framework may be brought into view by staining the cell with iodine when it appears as a number of deeply-staining granules which still mark out the boundaries of the separate mucilage-drops (Fig. 19). In the fresh and fully-developed cells, especially of the leaves (Fig. 20), it is often indistinguishable, but may be readily demonstrated by the use

of either iodine or osmic acid. The secretion is produced mainly at the expense of the endoplasm and of the substance of the plastids. As we have remarked before, the remains of the ectoplasm and nucleus may always be recognised, and they are usually left behind after the escape of the secretion (Figs. 27 and 29). The changes which occur in the drops themselves are of great interest. At their first formation the young drops are watery and by no means well defined. By the use of osmic acid it can be demonstrated that at this stage they contain no tannin. They shortly become denser and more highly refractive, and tannin makes its appearance equally distributed throughout their structure. Osmic acid then gives very striking results, for the separate drops are blackened by the reagent while the protoplasmic reticulum takes practically no stain, and thus the contrast between the two is sharp and well defined. And now in the drops themselves a delicate reticulation may be observed, which finally gives way to the appearance of numerous minute and brightly shining droplets, all separate and distinct, disseminated throughout the substance of the drop, just as the drops themselves are disseminated through the substance of the secretory protoplasm (Figs. 10 and 13). The droplets do not contain tannin, and osmic acid stains the ground substance only. We have thus been able to trace a wonderful series of changes, which must from a chemical point of view be of a most interesting character, but which at present we cannot with certainty explain. Methylene-blue confirms the results obtained with osmic acid. This substance, as Klebs[1] has shown, is capable of forming with tannin a definite compound: and we ourselves have observed that the staining produced by the dye in structures containing tannin is one which is both distinct and easy to be recognised, especially when viewed through yellow light, such as that produced by an argand burner. The coloration, namely, is a somewhat dull purple blue, not unlike that produced by haematoxylin, and stands out in marked contrast to the usual

[1] Klebs in Untersuch. a. d. bot. Institut z. Tübingen, 1886.

bright and pure azure of the normal methylene-blue stain. In the present instance the minute and brilliant droplets assume the clear azure colour, while the substance of the drop is of the dull murky purple to which we have already referred. We may pass on to other reactions of the mucilaginous secretion in the gland-cells. With iodine and chlorzinc-iodine (Schultze) it undergoes just the slightest blue coloration. With Hanstein's reagent it stains reddish purple, and with picronigrocin steel-blue. When carefully treated with Hofmann's blue it does not stain, and therein differs from the protoplasmic reticulum which colours well and becomes clearly demonstrated. With corallin-soda there is no conspicuous staining. The drops and droplets are but little affected by either hot or cold water beyond mere swelling, but they dissolve or rather become invisible in dilute potash, often leaving the protoplasmic reticulum exceedingly well defined.

We are at present unable to state with any definiteness what is the exact nature of the bodies produced during the various stages of secretion, but from the above reactions we believe that in the mature and fully developed drop the ground-substance consists mainly of gummy mucilage, while the droplets themselves consist of pure gum. The reaction with iodine and chlorzinc-iodine seems to indicate that the mucilage is allied to certain forms produced by the hydration of cellulose-structures. Thus the protoplasm gives rise to some body producing a gummy mucilage, and the latter is further split up into a gum and a gum-mucilage residue. The reticulation which appears in the young drop, and precedes the formation of the droplets, is a phenomenon of great interest, and seems to indicate that the substance first produced by the protoplasm is in a state of high organisation, if not actually living; but this can only be settled by careful observation and elaborate experiment. At present we have no data which throw any further light upon the subject.

With alcohol or with plasmolysing reagents the whole mucilaginous contents undergo great contraction but return to their normal bulk upon the careful addition of water. Plas-

molysis also affords striking proof that the mucilage is entirely contained in the endoplasm and does not arise from the cell-membrane, for at any stage during secretion the protoplasmic body may be withdrawn from the wall to which it is always connected by numerous fine fibrils and delicate threads, and it can then be plainly seen that the whole of the mucilage is included within the shrunken utricle (Figs. 22 and 23).

From the point of view of visibility both the drops and droplets vary considerably. In some glands where the mucilage is dense and the protoplasmic reticulum well defined, the structure is very obvious without any special preparation (Figs. 5, 6, 10). In other cases the reticulum appears to be less marked (Fig. 20), the mucilage less dense, and the droplets but feebly defined and little developed. Such glands require careful observation, and a cautious and well-regulated use of reagents, to demonstrate that their actual structure is that which we have described. Other glands appear to form an abnormal amount of tannin (Figs. 24, 25 and 26), and these are the most difficult to deal with. The drops and droplets are never so clear in this case and are sometimes even scarcely to be distinguished. Finally, and as a very common phenomenon, there is a marked difference in appearance between the cortical and peripheral mucilage (Figs. 7 and 8). This is mainly due to the difference in pressure with which the two systems meet. The first-formed drops bud out freely into the cell-cavity, while those produced later on, by the repeated basipetal formations, come into existence when the cell is fairly full of drops, and are thus soon exposed to great pressure on all sides, and being densely packed appear to be more highly refractive than those of the central core. Apart from this, the structure of both forms appears to be quite similar, but the density of the drops and droplets varies greatly.

The cell-contents usually escape by means of a small localised rupturing of the wall (Figs. 9 and 27), and the various drops are turned out, both by the elasticity of the wall, the feeble contractility of the ectoplasmic remains, and

by the swelling of the mucilage both of the inner layers of the cell-wall and of that of the drops themselves. The combined effect of these various forces produces a very practical result, and the drops escape with some rapidity from the ruptured gland. In ordinary circumstances water penetrates with great difficulty through the cuticularised wall. Thus we found, when testing with osmic acid, that the reagent penetrated by means of the basal transverse wall and by way of the stalk-cell infinitely sooner than through the exposed cell-membrane. When therefore a rupture occurs, there is quite a rush of water and great swelling of all the mucilaginous structures. Another mode of escape also occurs (Fig. 28). In this case there is no rupture in the real sense of the word, and the phenomenon only takes place in old cells which have hitherto remained imperforate. The whole wall through disorganisation gradually breaks down on all sides and the swollen drops quietly escape.

We have yet to mention a small matter of some interest in connection with the mucilage-glands, and this is that in *Blechnum occidentale* we always found a fungus associated with the growing point. The growth of the mycelial filaments proceeds *pari passu* with that of the young shoot, and even manages so to distribute the numerous hyphal branches over all the young structures that, by the time the various mucilage-cells are ready to rupture, there is always some attendant hypha near at hand. As soon as the contents have escaped, this hypha grows into the ruptured cell by means of the orifice and soon makes strong growth, obtaining apparently much sustenance from what remains of the ectoplasm and nucleus (Fig. 30). We have not cultivated this fungus and are consequently unable at present to state any further details.

Before concluding our description of *Blechnum occidentale* we may perhaps make some remarks concerning the resin-gland-cells. We have already described their development and stated that their structure is somewhat simpler than that of the mucilage-glands. It is a matter of great interest that

in the same plant, and even on the same scale, there should be two forms of hairs practically identical in development, distribution, and even in their broad plan of structure, one of which should secrete mucilage, and the other, by some difference (possibly a slight one) in the metabolism of its protoplasm, should give rise to resin. It is a phenomenon which is certainly worthy of more investigation, but for the present we have confined ourselves to the question of mucilaginous secretion, and we can now do no more than give just the slightest description of the structure of the cells and the mode of secretion of the resin. Each cell contains a lenticular and very distinct nucleus, and the protoplasm is exceedingly granular in the functional cells, especially towards the head, where the nucleus and the main mass of the protoplasm is situated (Fig. 32). A single large vacuole is generally present at the base of the cell, and here the utricle is thinner and hyaline. The secretion collects only under the head of the gland, so that the bladder does not surround the whole free surface (Fig. 31). The resin gives the usual reaction with alcannin, and in certain cells it was recognised both under the cuticle and in the cell-contents. We think there is little doubt that the mode of development of the resin is similar to that of the mucilage, and that some formed body, produced by the activity of the protoplasm, is present as a series of metaplasmic drops, and undergoes further changes before the final production of resin.

(b.) Osmunda regalis, L.

We have seen that in *Blechnum occidentale* the young bud is adequately protected both from mechanical injury and also from abnormal variations of temperature and moisture by the numerous paleae and by the secretory hairs of the paleae and leaves. In *Osmunda* a similar provision occurs, but the details of the arrangement are somewhat different. In this case paleae are absent, and it is the base of the leaf-stalk, here winged and sheath-like, which acts as a protection against injury from without and also bears the mucilage-cells (Fig.

33)[1]. No resin-secreting hairs are present, and on the young lamina only woolly hairs are to be found. The mucilage-glands occur on both sides of the young leaf-base, and are unbranched and filamentous. All the cells of the filament are usually glandular, so that, unlike *Blechnum occidentale*, there is here a row of secreting cells and not a single terminal gland (Fig. 34). The non-secreting woolly hairs are long and branched, and cover the young lamina with a dense felt which affords an excellent protection against extremes of temperature (Fig. 35). The development of both forms of hairs is essentially the same, and it is only in their subsequent behaviour that they so markedly differ. They first arise as outgrowths of epidermal cells which are subsequently cut off by a wall from the general cell cavity (Figs. 38 and 39). The small cell thus produced is the mother-cell of the hair, which soon divides freely and produces a long filament (Fig. 34). In the case of the mucilage-hairs the growth is strictly basipetal, and the hair is almost always simple and unbranched. The woolly hairs on the contrary may also elongate by means of apical growth, and branching with them is the normal and usual phenomenon. The young cells contain each a nucleus, usually provided with two, or sometimes three, well-marked nucleoli, and several plastids.

As the cells grow they gradually become vacuolated, and, as in *Blechnum*, the nucleus is situated on the inner side of the ectoplasm in the mature cell. At an early stage the plastids divide and soon produce numerous starch-grains (Figs. 34 and 35), which in the young cells occur in the bridles of protoplasm stretching from the nucleus, and, later on, become distributed all round the primordial utricle. They then occupy a position similar to that of the nucleus.

[1] According to Prantl (see Sadebeck in Schenk's Handbuch, Bd. i. p. 274) the outermost young leaves of each winter-bud become peculiarly modified and scale-like, having for their function the protecting of the youngest and innermost members. Since our research was undertaken in October 1886 and finished in April 1887, we were working principally upon winter-buds provided with the modified leaves.

We may now confine ourselves to the consideration of the secretory hairs, dealing with the woolly hairs later on. The free walls of the mucilage-cells become markedly cuticularised but the transverse walls undergo a mucilaginous change. It soon becomes manifest that they also experience a great increase of thickness on either side, and reagents demonstrate that the thickening layers are of the nature of callus. Further, one can observe a phenomenon of great interest, for both the wall and the callus-layers on either side are perforated by a number of fine holes, which may be readily recognised even by direct observation and without the use of reagents (Figs. 36, 41, 43). A similar perforation of the transverse walls has already been described by Behrens[1] as occurring in the secretory hairs of *Ononis spinosa*, but in this case there is no callus present. The structure presented by *Osmunda regalis* is very like that of certain forms of callosed sieve-tubes, and in its mode of arrangement —the transverse wall and its two callus-plates—it even more strongly resembles that described by Schmitz[2] for so many of the Florideæ. We think it hardly necessary to refer at any length to the importance of these perforations in establishing a continuity of the protoplasm between the various adjacent filament-cells, since one of us[3] has already treated of the subject in some detail, but we would only wish to point out that its existence affords yet another proof of the porosity of the cell-wall, and of the very intimate connection which probably exists between all the constituent cells of living plant-tissues. The mucilaginous and callosed wall also serves a most important function in connection with the discharge of the secretion, for whereas the cuticularised walls are both resistent and impervious, the transverse membranes readily take up water, and, rapidly swelling on all sides, they finally cause the rupture and separation from one another of the secretory cells of which the adult

[1] Behrens in Ber. deutsch. bot. Gesellschaft, Bd. iv (1886), p. 402.
[2] Schmitz in Sitzber. Akad. Wiss. Berlin, 1883, p. 215.
[3] Gardiner in Arbeit. a. d. bot. Institut z. Würzburg, Bd. iii. p. 52.

hair is composed, and the escape of the mucilaginous contents is then a very easy matter (Fig. 44). In certain instances, however, the rupture and escape takes place as in *Blechnum*.

The mucilage of the mature glands when examined in water appears dense and horny. As in *Blechnum brasiliense* there is a marked distinction between the looser and more granular central core (Fig. 40) and the highly refractive and lamellated peripheral portion of which the bulk of the secretion consists. On the addition of alcohol the layering becomes much more evident, and at least three well-defined zones may then be distinguished (Fig. 43); the peripheral portion, already referred to, undergoing further differentiation into two or more concentric strata. This separation into layers evidently depends upon the constitution and tension of the various parts of the mucilaginous secretion. The centremost portion represents the first formed mucilage as in *Blechnum brasiliense*. The most external and densest layer is, on the contrary, of the more recent formation. It is exposed to some pressure and it differs also in constitution, since, as we shall see further on, starch largely enters into the composition of it. The middle zone consists of mucilage practically free from starch, being derived purely from the inner portions of the endoplasm; and here the pressure is the greatest of all, since it is situated between the central core which, being most disorganised, swells to the maximum and refuses to yield, and is also exposed to the pressure of the outer zone in which new drops are continually being formed and pushed towards the centre. See also Fig. 40, which shows relative pressure of drops.

We may now describe the mode of secretion. If in *Blechnum brasiliense* it appears that the mucilage is partly derived from the cell-wall, so much the more is this the case in *Osmunda*, where even the layering which accompanies ordinary mucilaginous degeneration is wonderfully simulated (Fig. 44). Goebeler[1], indeed, actually states that the mucilage

[1] Goebeler, loc. cit.

does arise from the inner layers of the cell-membrane, but de Bary[1] with his customary caution merely remarks that 'the origin of this mucilage has yet to be investigated.' As a matter of fact the development is precisely similar to that which we have described in *Blechnum*. Here also the secretion arises in the form of isolated drops, which at first bud into the cell-cavity, and are subsequently increased basipetally until the cell is full (Fig. 40). In *Osmunda* the drops are both smaller and more numerous. In each drop a further differentiation into droplets takes place, but the comparative difference of density of the two structures is not nearly so great and as a consequence the droplets are somewhat difficult to define, but by appropriate swelling in water and staining in methylene-blue the whole structure may be clearly seen. In the denser peripheral mucilage even the drops themselves are difficult to distinguish without preparation, and the protoplasmic framework is slight and fine. Neither chromic nor osmic acid can be employed for the examination of the fresh hairs on account of the enormous quantity of tannin, which stains the whole structure so deeply as to render satisfactory observation quite impossible. Iodine gives striking and beautiful results, and, as our figure (Fig. 40) shows, one may bring out in the mature cell the nucleus, the drops, and the framework with great distinctness and effect. See also Fig. 41, where the drops are seen from the outside. The secretion of the drops commences in very young cells, and some of the drops first formed appear to burst into the cell-vacuole as in *Blechnum*. For a long time the starch, which is present in the cell in great quantity, takes no active part in the drop formation, but, as the zone of secretion spreads, they gradually break down and disappear. The degeneration, both of the starch grains and of the nucleus, is usually accompanied by the frothy and utriculated appearance which characterises such degenerations as that of the chlorophyll-corpuscles of *Chara*

[1] De Bary, loc. cit.

when caused by the action of water, and it is often a matter of difficulty during the later stages of secretion to distinguish the bubble-like appearance connected with the true drop-formation from the somewhat similarly utriculated starch-grains, and portions of the nucleus also. In no case does the whole of the nucleus disappear, but the starch-grains become entirely disorganised and destroyed. Not unfrequently irregular lumpy masses of callus occur on the side walls of the cell, and equally with the callus of the transverse walls they appear to be formed, at least partly, from the starch-grains; thus confirming the view that callus is of the nature of a starchy mucilage[1].

The mucilage of *Osmunda* is of the same nature as that of *Blechnum*, and gives similar reactions. Certain phenomena occur in consequence of the action of corallin-soda, which are perhaps deserving of mention. In the first place, the protoplasm adheres with great tenacity to the transverse walls, and, even after death, the main protoplasmic body is connected to them by numerous fine filaments. This is of some interest in connection with the perforation of which we spoke. Secondly, a number of delicate utricles arise on the free surface of the protoplasmic body; these appear to owe their formation to an external secretion of mucilage, induced by the deleterious action of the somewhat concentrated solution of sodic carbonate (Fig. 42).

We have already alluded to the mode of rupture of the cells and the escape of the secretion. The mucilaginous contents escape in one large mass, which soon swells and disorganises. Very commonly the ectoplasm and what is left of the nucleus remain in the cell after the secretion has escaped, and thus afford further proof that all the mucilage is derived directly from the endoplasm and is enclosed by the ectoplasm. The protoplasmic framework breaks down and becomes granular as in *Blechnum*. The amount of slimy and stringy mucilage, which results from the addition of water to the free secretion,

[1] Gardiner, in Camb. Phil. Soc. Proc., vol. v (1883), p. 230.

is perfectly enormous and much greater in quantity than in *Blechnum*. In *Osmunda* no fungus was found to accompany the young leaves, the increased amount of tannin being perhaps unfavourable to the mycelial growth.

The fate of the woolly hairs is quite different from that of the glands, notwithstanding the similarity in the mode of development. Their cell-wall, which in the adult cells is often of very appreciable thickness, permanently retains its cellulose character and does not become cuticularised. The starch-grains gradually disappear from the mature cells, and on some of the transverse walls a callus may occur. In many of the cells the contents especially devote themselves to the formation of tannin, in which case they appear clear and highly refractive. In the very oldest cells the contents entirely disappear. With these remarks we end our description of *Osmunda*.

General Results.

The secretory hairs which we have now described are characterised by a peculiarity rarely met with in glandular trichomes, in that the secretion does not leave the cell but remains included in the protoplasmic body throughout its entire life. The continuous aggregation, the manner of secretion, and the dense and solid character of the substance thus formed, enable us to understand how it is that in these particular glands the structure is clear and well-defined.

The secretion commences by the breaking down of a portion of the innermost layers of the endoplasm at a number of contiguous but isolated areas. The first secretion occurs just beneath the free surface, and takes place equally around the whole cell-cavity, and the phenomenon steadily continues from within outwards, extending to deeper and deeper layers, until the whole of the endoplasm, together with the substance of the plastids, have taken their share in the process. We are unable to state whether these changes are limited to the endoplasm only, since the exact boundary between the ectoplasm and endoplasm cannot be defined. In the present state

of our knowledge we should not think it well to attempt to separate too sharply the structures which we have hitherto regarded as merely differentiated parts of the same body, and we would therefore prefer to state the case thus: that whether the ectoplasm contributes or not to the secretory changes, yet in all cases a very conspicuous portion of it remains, which is associated also with the remains of the nucleus.

In the special instance before us the vacuole does not persist for any length of time, for its cavity soon becomes obliterated; in the first place, in consequence of the very voluminous character of the secretion, and subsequently, because of the disorganisation of the bounding membrane (hautschicht) which until then had shut off the contents of the vacuole from the general protoplasmic body. The secretion, as we have seen, is not turned out of the cell, but continually collects and aggregates, and its remarkable swelling properties cause it to become very bulky, and to take up the whole of the available cell-space. It would, perhaps, appear at first sight that the vacuole takes some definite part in the secretory changes, but bearing in mind the mode of first formation, and taking into consideration the phenomena which occur in other secretory cells, we are led to conclude that the secretion is strictly intra-protoplasmic, and that neither the vacuole nor its contents take any direct part in the actual secretory process[1].

We found that the secretion was produced as a number of isolated drops, and we have just explained that they are situated *in* the substance of the protoplasm. They are doubtless produced as a result of katabolic change, and must be regarded as coming under the head of metaplasm or formed substance. We have described in detail the sequence of

[1] A secretion being once formed, it may of course pass either to the exterior or interior of the cell. We have examples of both cases in *Blechnum occidentale*, for in the mucilage-hairs some few of the drops escape into the cell-vacuole, and in the resin-hairs the secretion passes to the outside and appears beneath the cuticle. We may add here that what is true of the special substances which we are accustomed to regard as secretions or excretions *par excellence*, e.g. oil, resin, &c., is probably true also of many other substances, nutritive and non-nutritive, which occur in the cell-vacuole.

changes which ensue during their secretion, and we found that the drops appear to consist in the first instance of a clear gummy mucilage. This substance experiences further change, and in the fully developed structure we are able to distinguish, in each drop, a number of secondary spherical droplets which now give the reactions of pure gum. Thus the protoplasm gives rise to a gummy mucilage, and the latter undergoes further differentiation into a ground-substance, which still retains its mucilaginous character, and into a gummy substance (the product probably of maximum chemical change) which is present as a number of isolated spherical droplets.

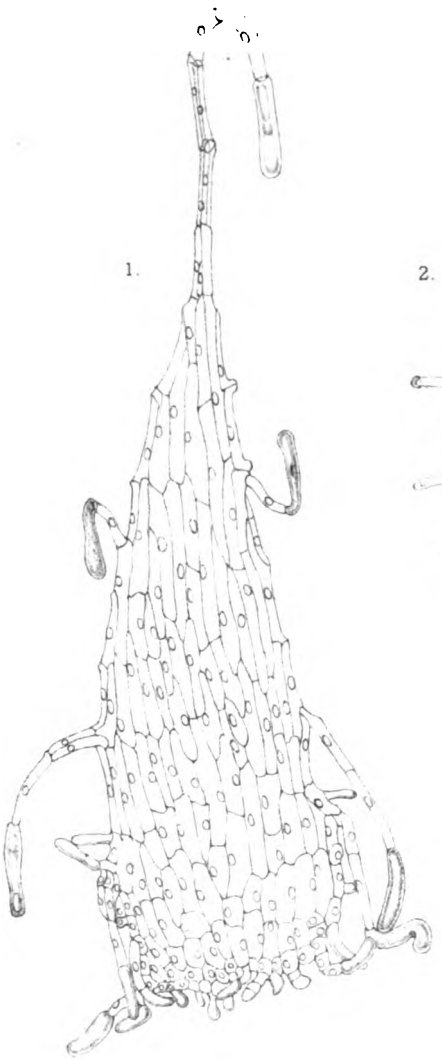
In the mature gland the various drops are disseminated throughout the substance of the protoplasm, so that the protoplasm itself appears as a delicate reticulum or framework which contains the various drops in its meshes. It is a point of great interest to us that our results tally in a most remarkable manner with those obtained by Langley, in his research on the structure of animal secreting glands. We may even compare his description with our own, and if we provisionally eliminate from consideration the cell-wall, the cell-vacuole, and the plastids as being especially associated with plant cells, it will be seen that there is a great similarity between the two structures. The particular paper we quote from appeared in the 'Proceedings of the Cambridge Philosophical Society[1].' We necessarily somewhat condense Langley's remarks. He writes, 'The secretory glands have the following common points of structure. The cell substance is composed of (*a*) a framework of living substance or protoplasm, connected at the periphery with a thin continuous layer of modified protoplasm[2]. Within the meshes of the framework are enclosed two chemical substances at least, viz. (*b*) a hyaline substance in contact with the framework, and of (*c*) spherical granules which are imbedded in the hyaline substance.' We do not wish to press the similarity too far, since we are aware that in establishing comparisons between

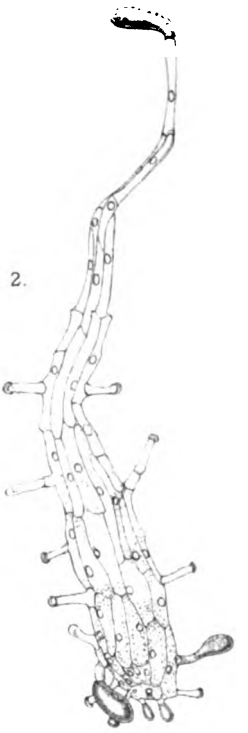
[1] Langley in Proc. Camb. Phil. Soc., Vol. v (1883), p. 25.

[2] Our ectoplasm.

representatives of the Animal and Vegetable Kingdoms great caution must be observed. But we are nevertheless of opinion that a distinct unity both of plan and structure underlies all the similar phenomena common to the two great classes which constitute living beings, and that any apparent difference is one of degree and not of kind. In the case of certain animal glands, e.g. serous and mucous salivary glands, Langley concludes that the protoplasm forms the hyaline substance, and then out of this manufactures the granules which, during secretion, are turned out of the cell and give rise to the particular substance which the gland happens to secrete. The state of active secretion is followed by a period of rest during which the protoplasm grows, forms new hyaline substance, and from this again are produced new granules. We believe that a series of changes essentially similar in character obtain in certain plant-cells also. Usually speaking, plant-cells are incapable of such active and repeated secretion as occurs in those of animals, and in many instances, e.g. *Blechnum occidentale* and *Osmunda regalis*, the secretory changes occur in the cell once and for all, and at their termination the cell dies. But in other glands, e.g. those of *Drosera*, it appears exceedingly probable that the phenomena which accompany the repeated secretion are quite identical with those which happen in so many animal glands.

We have seen that, in the two mucilage-glands investigated by us, the secretion is not turned out of the cell during its lifetime, but in such cases as the resin-glands of *Blechnum occidentale*, where the secretion normally escapes, we may endeavour to offer some explanation as to the way in which the passage of the secretion to the exterior is brought about. For this purpose we may conveniently divide the secretions into (1) soluble and (2) insoluble substances. The soluble probably simply pass through the substance of the protoplasm by diffusion, but we must not omit to state that during this process the external membrane (hautschicht), the ectoplasm, must undergo some decided modification or change in relation to such special phenomenon. The insoluble secretions on the





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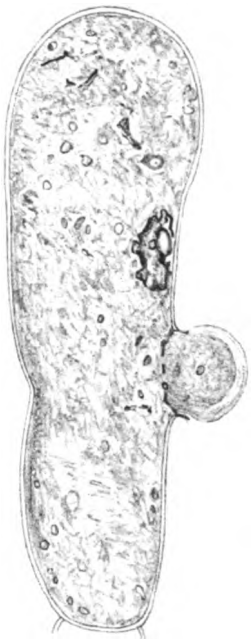

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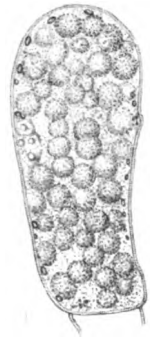

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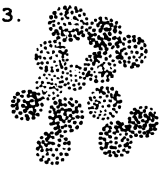

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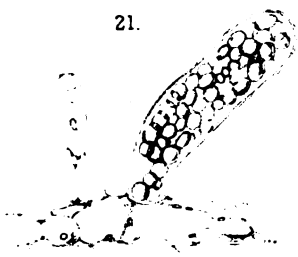

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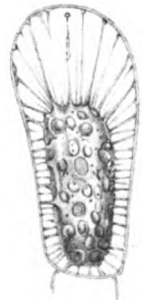

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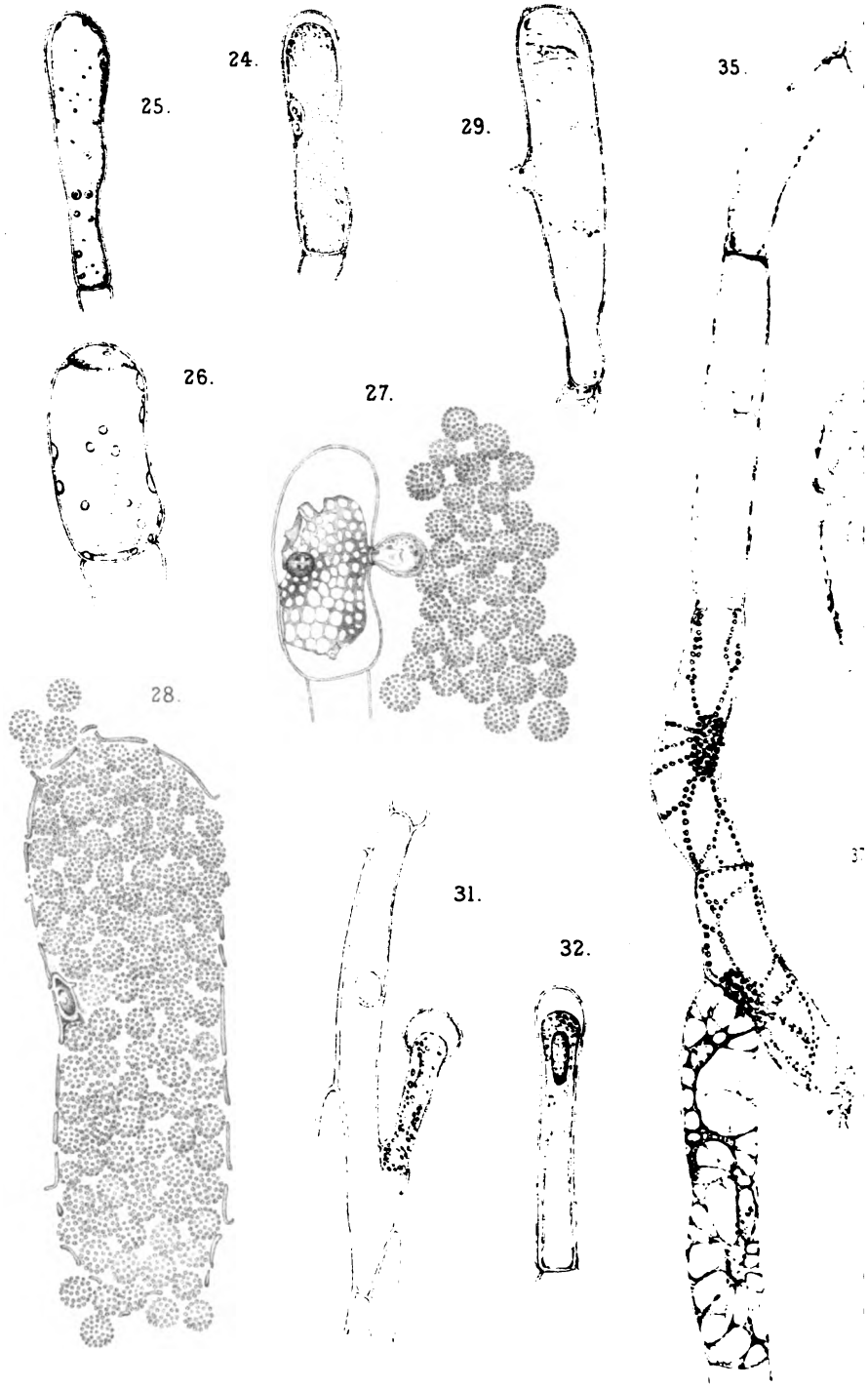

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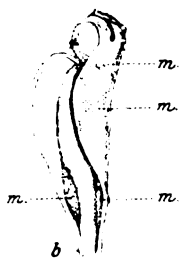

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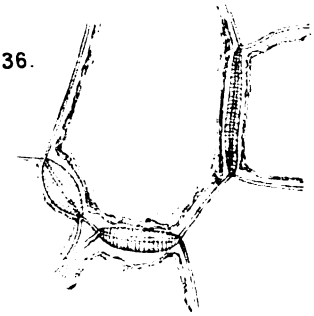

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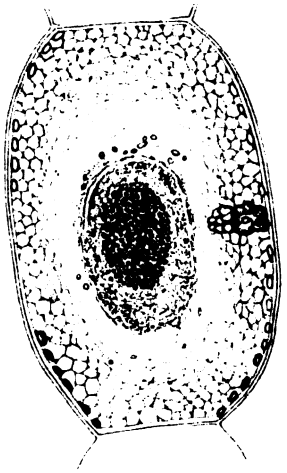

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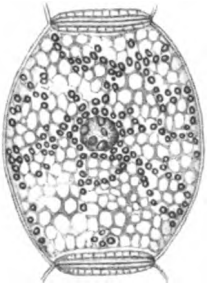

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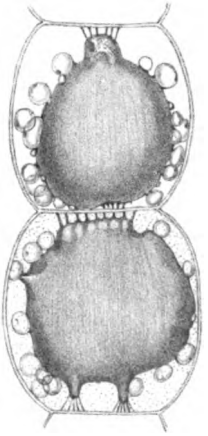

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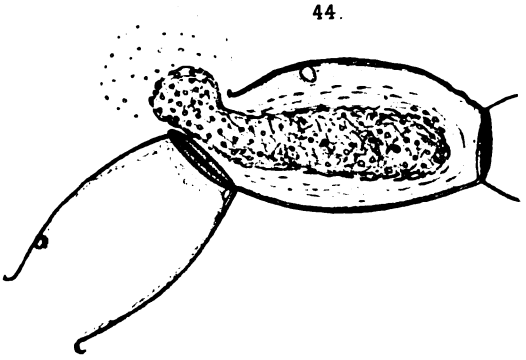

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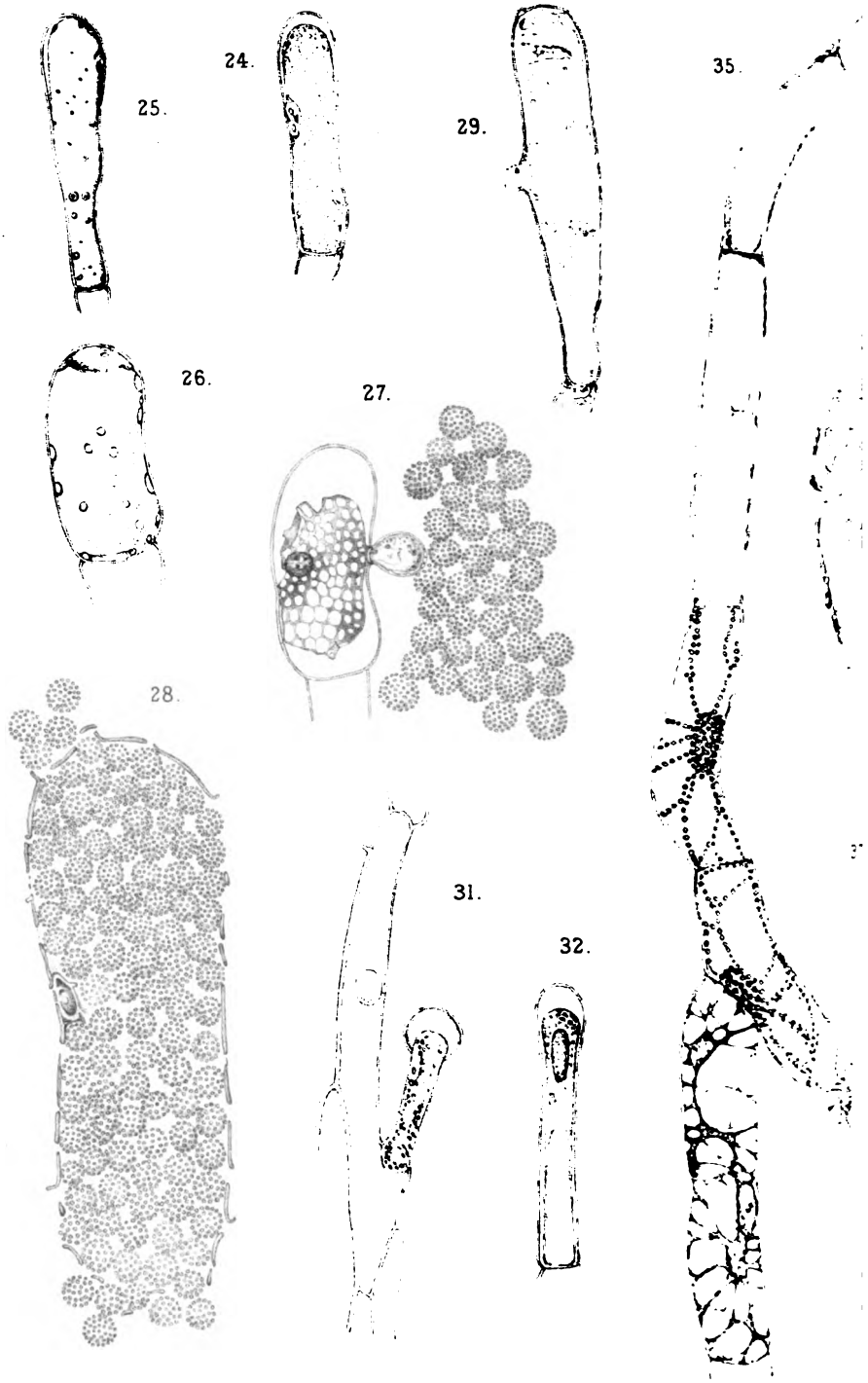

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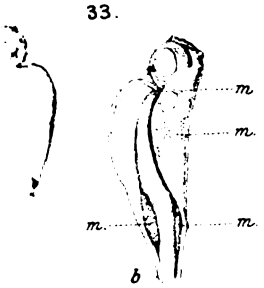

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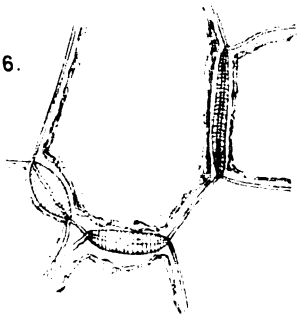

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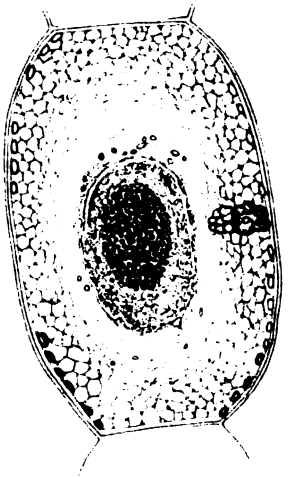

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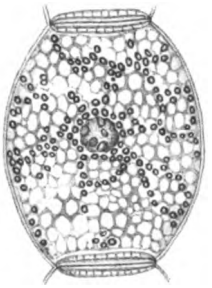

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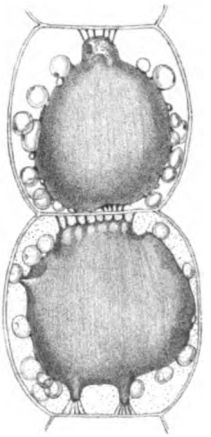

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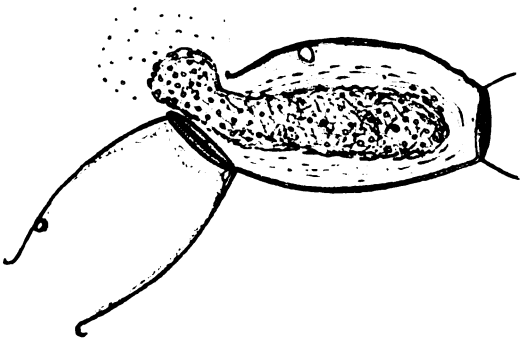

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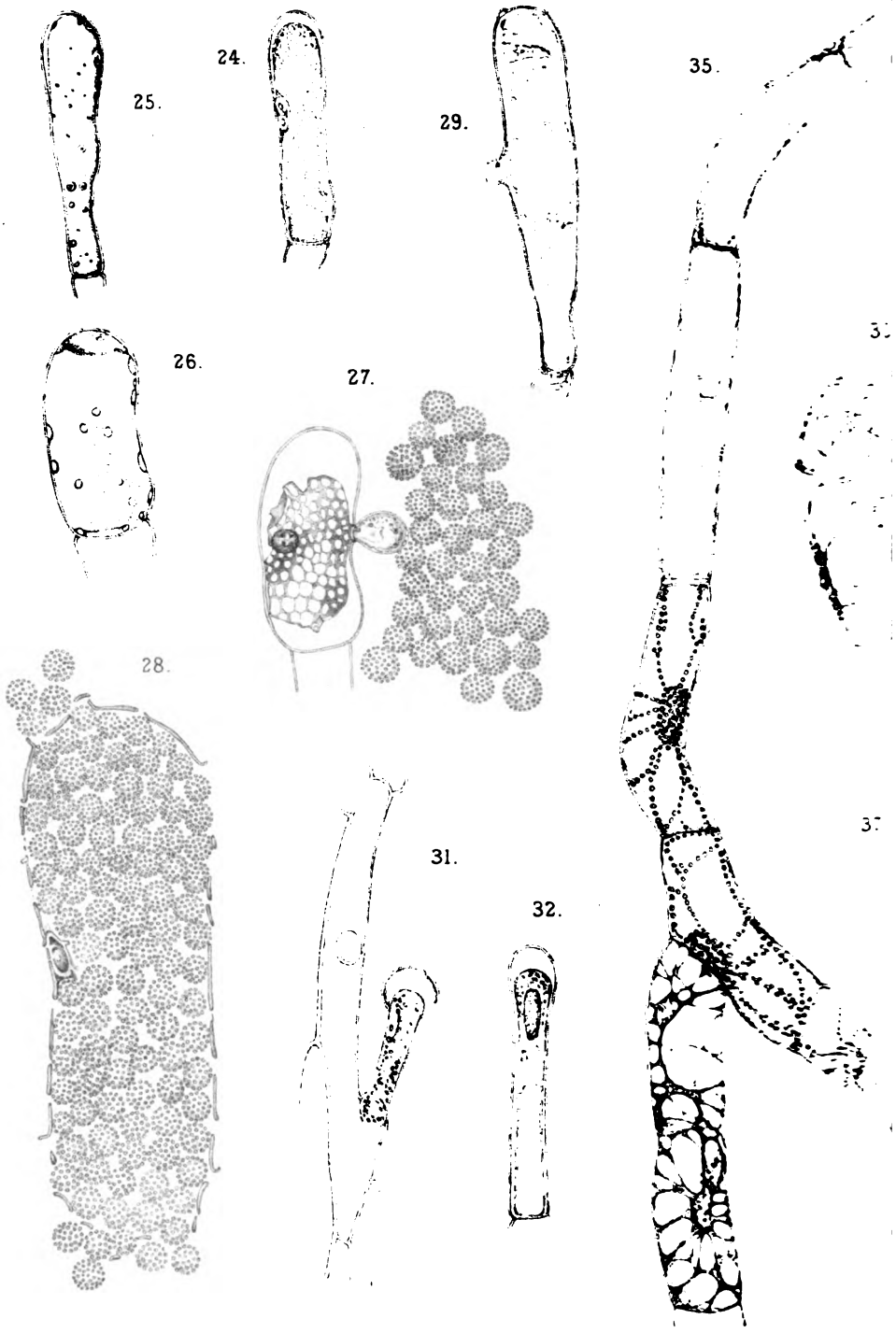

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GARDINER & ITO.— ON MUCILAGE SECRETION.

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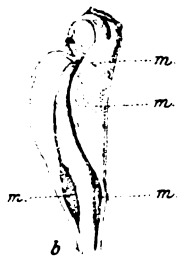

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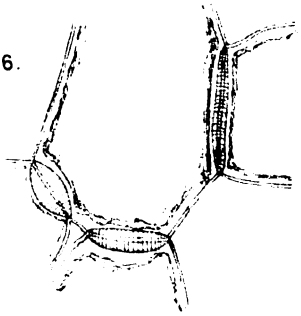

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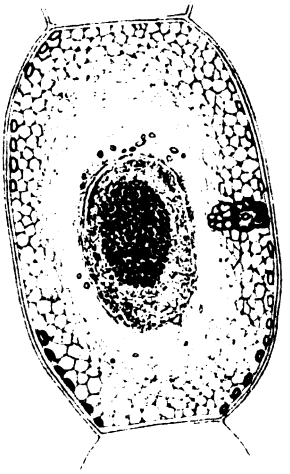

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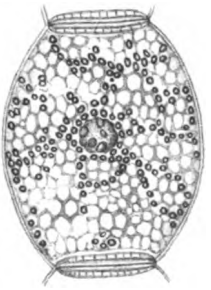

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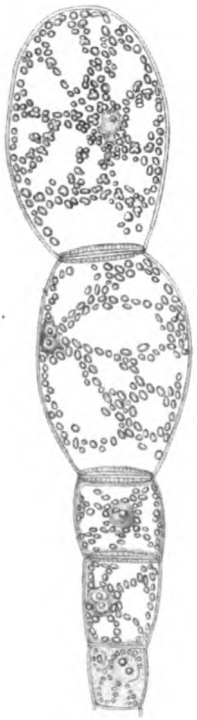

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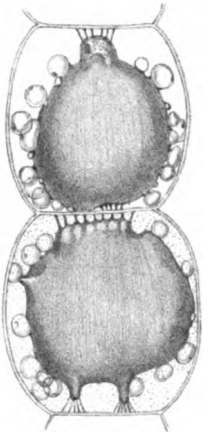

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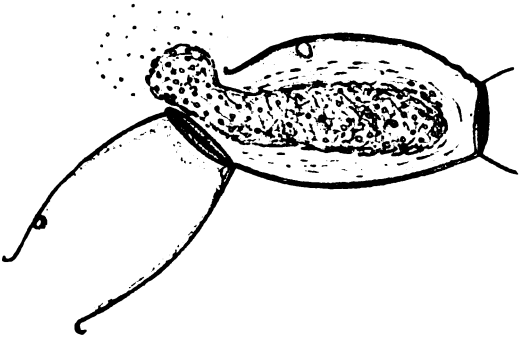

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other hand have to work their way bodily through the protoplasmic membrane in order to escape to the exterior. This is probably brought about by a series of actual minute rupturings of the substance of the protoplasm, which no doubt at once heal, and the final escape to the exterior is possibly attended by the production of inflated bubbly protrusions, which burst in a manner essentially similar to that which occurs in the young cells of *Osmunda* and *Blechnum* in the case of certain of the first formed mucilage-drops. The passage through the cell-wall is a comparatively easy matter. Whether or not the cuticle is raised depends upon the density of the secretion and the degree of cuticularisation. Should the secretion, instead of escaping to the exterior, pass into the vacuole the phenomena are quite similar in detail, except that the inner membrane (hautschicht) of the endoplasm instead of the external membrane of the ectoplasm would have to be taken into account.

BOTANICAL LABORATORY, CAMBRIDGE,
May 26, 1887.

EXPLANATION OF FIGURES IN PLATES III & IV.

Figures 1–32 illustrate *Blechnum occidentale*, except Fig. 4 (*Ceratopteris thalictroides*) and Fig. 7 (*Blechnum brasiliense*). Figs. 33–44 illustrate *Osmunda regalis*.

(Where not otherwise stated the drawings are taken from fresh specimens.)

Fig. 1. One of the paleae from the young shoot bearing numerous mucilage-glands.

Fig. 2. A similar palea bearing resin-glands.

Fig. 3. Apical portion of a very young bud, showing the young mucilage and resin-cells developed from the epidermal cells.

Fig. 4. Early stages in the development of *Ceratopteris thalictroides* (after Kny). The terminal cell which will become the mucilage-gland is already well developed.

Fig. 5. Mucilage-gland from young leaf representing the 'clear-drop' stage of the mucilaginous contents.

Fig. 6. A slightly older gland. The drops appear to have clubbed together into an irregular lobular mass. Reagents, or even careful examination of fresh material, show that the drops are in reality quite distinct from one another. The drops display a distinct granulation.

Fig. 7. Mature gland of *Blechnum brasiliense*. The contents show a differentiation into central, dark and granular core, and a clear and highly refractive peripheral portion, which exhibits signs of layering.

Fig. 8. Similar cell from the leaf of *Blechnum occidentale*.

Fig. 9. Terminal mucilage-gland from a palea, showing the granular mucilaginous contents which apparently possess quite a homogeneous structure. In spite of the disorganisation, on account of the complete breaking down of the endoplasmic framework, the mucilage is still present as a number of isolated drops. These may be demonstrated by swelling with water, and staining with methylene-blue. Note the disintegrated nucleus and the mode of rupture.

Fig. 10. Gland from leaf. The drops exhibit differentiation into droplets. The nucleus and plastids are fairly well shown.

Fig. 11. A similar gland from a palea.

Fig. 12. A similar gland from leaf at a later stage than Fig. 10.

Fig. 13. Several isolated drops from a leaf gland.

Fig. 14. Early stage in the development of gland-bearing hair. The terminal cell is that which becomes converted into the mucilage-gland.

Fig. 15. Older gland-cell. Note the nucleus, the plastids, and the strands of protoplasm stretching from the nucleus. Vacuolation is now well marked.

Fig. 16. Gland from young leaf treated with osmic acid. The first formation of the young mucilage-drops may be observed taking place around the primordial utricle, and in the strands of protoplasm. Certain of the contents of the vacuole of a mucilaginous nature have become contracted by the action of the reagent.

Fig. 17. More advanced gland. The drops now numerous, and some even show the droplet stage. The basipetal formation of new drops is in this instance shown very clearly.

Fig. 18. Young cell after treatment with chromic acid. The clear spaces which mark the points of origination of the drops are seen from the outside. The half-dozen or so of the very clear circular spots, although they simulate the true formation, are in reality produced in consequence of the shrinking of the protoplasm from the wall at several small isolated areas, through the dehydrating action of the reagent employed. The impermeability of the mucilaginous cell contents causes the penetration of the reagent to take place with great difficulty, and often forces the protoplasm to give way.

Fig. 19. Gland from leaf containing drops which exhibit but little definition. Note the nucleus and the protoplasmic framework. This gland was stained with iodine.

Fig. 20. Similar gland with unusually clear contents. Drawn from fresh material mounted in water.

Fig. 21. Two glands from young leaf. The smaller is a resin-gland. The larger secretes mucilage, and shows the 'clear-drop' stage.

Fig. 22. Young gland after treatment with ten per cent. sodium-chloride-solution.

Fig. 23. Older gland similarly treated. In this the drops were in process of formation.

Fig. 24. Gland in which the protoplasm has formed an unusual quantity of tannin. In osmic acid.

Fig. 25. A similar gland in its fresh state.

Fig. 26. A gland of the same nature as Figs. 24 and 25. Note the formation of drops and the peculiar position of the nucleus.

Fig. 27. Mucilage-gland undergoing rupture. The remains of the nucleus and ectoplasm continue in the cell. The ectoplasm still shows on its membrane traces of the reticulation and arrangement associated with the formation of drops. In osmic acid.

Fig. 28. Second mode of escape of secretion. See text.

Fig. 29. A cell after the escape of secretion. Remains of ectoplasm apparent.

Fig. 30. Ruptured gland, showing fungus-mycelium which is now feeding on the remains of the ectoplasm.

Fig. 31. Resin-gland from palea. The secretion is collected under the raised cuticle. In osmic acid.

Fig. 32. Resin-gland after treatment with picronigrocin. Note the lenticular nucleus and the protoplasm which is collected towards the cell-apex, and there exhibits marked granularity.

Fig. 33. Two views of a very young leaf of *Osmunda regalis*: *m* = the places where the mucilage-hairs are to be found in the greatest number.

Fig. 34. Young mucilage-secreting hair. The cells are in various stages of development, and the growth is markedly basipetal. The starch-grains are especially situated in the protoplasmic strings, and in the upper cells the callosed and perforated transverse walls may already be observed.

Fig. 35. Young woolly hair. In the clear cells towards the apex the cells are particularly rich in tannin. (This hair is taken from a leaf which had been for a short time removed from the plant. The peculiar aggregation of the starch-grains in the protoplasmic strands is somewhat abnormal. In quite fresh cells they are found around the primordial utricle. Fig. 34 has also been somewhat affected by the treatment to which it was subjected.)

Fig. 36. Portion of a branched mucilage-secreting hair, showing the transverse walls and the two callus-plates belonging to each. The whole system (walls and callus) shows perforation.

Fig. 37. Portion of a young woolly hair cell with callus well developed on one side of the transverse wall.

Fig. 38. Young stage of development of mucilage-hair.

Fig. 39. Slightly older stage.

Fig. 40. Semi-diagrammatic optical section of mature mucilage-cell after treatment with iodine. Note the differentiation into layers, the drop-formation, the protoplasmic reticulum and the disorganised nucleus.

Fig. 41. A similar cell from the outside. The mode of drop-development is quite apparent from this point of view. Some of the reticulation and formation of circular areolae is due to the disorganising starch-grains. The distinction between

the two cannot be conveniently shown in a drawing, but may be recognised with care, in the actual preparations, by the use of reagents.

Fig. 42. Mucilage-cells after lengthy treatment with thirty per cent. solution of sodium-carbonate. The protoplasm withdraws with difficulty from the transverse walls, and is still connected with that structure by means of numerous delicate strands. Numerous external utricles have been produced by the action of the reagent.

Fig. 43. A mature cell after treatment with alcohol, showing the layering which is now so markedly demonstrated.

Fig. 44. Usual mode of rupture of mucilage-cell.

On Laticiferous Tissue in the pith of Manihot Glaziovii, and on the presence of Nuclei in this Tissue.

BY

AGNES CALVERT

AND

L. A. BOODLE, A.N.S.S.

With Plate V.

I.

IN April 1884 Dr. D. H. Scott published the results of his investigations on the Laticiferous Tissue of *Manihot Glaziovii*[1], showing that in this plant the laticiferous tubes, unlike those of the Euphorbiaceae previously investigated[2], are formed by the fusion of rows of cells. The two systems of laticiferous vessels, already distinguished by Trimen, were described, one being derived from the hypodermal layers of the external cortex, while the other is developed in the phloem.

In repeating some of these investigations, under Dr. Scott's superintendence, we found a third system, which occurs in the pith.

Transverse sections through internodes where secondary thickening has made some progress show that the peripheral part of the pith has thinner walls and contains more abundant starch and other cell-contents than the rest of the pith. It is

[1] Quart. Journ. Microscop. Science, vol. xxiv. pp. 194–204.

[2] Cf. De Bary, Comp. Anat. of Phanerog. and Ferns, Eng. ed., p. 437.

Annals of Botany. Vol. I. No. I. August 1887.]

to this part that the laticiferous tubes are confined. They usually occur in groups, each in the neighbourhood of a primary xylem-bundle (Figs. 1 and 3).

Bounding each primary xylem-group internally a tissue is frequently found consisting of thin-walled cells, small in transverse section, but considerably elongated longitudinally; these may be identical with the internal 'cambiform' cells described by Pax in several tribes of the Euphorbiaceae as representing rudimentary phloem[1]. They differ widely in shape from the thin-walled peripheral pith-cells described above, being longer and narrower, and rectangular in longitudinal section. The thin-walled pith forms an unbroken ring and lies inside these groups of cambiform cells.

Longitudinal sections show that the laticiferous tubes in the pith have reticulate anastomoses similar to those described by Dr. Scott[2] in the cortex; such a system could not arise from the branching of single cells. In the secondary phloem new laticiferous elements are continually being formed by the cambium, and in this region remains of the walls, separating the cells from which the laticiferous vessels are formed, were frequently found both by Dr. Scott and ourselves. In the case of the medullary tubes, stages in the absorption of the cell-walls could naturally only be observed near the apex of the stem, where the tissues have not yet passed into their permanent condition. Such stages were observed in parts of the stem about 2½ millimeters in diameter at a distance of 15–20 mm. below the apex. Fig. 8 shows a tolerably simple case of cell-fusion, in which the remains of a partially absorbed wall are seen.

Transverse sections through an internode show that the members of one group branch and anastomose freely among themselves, but do not anastomose with the members of other groups. The cortical tubes, on the contrary, form a continuous reticulate cylinder extending all round the stem[3].

[1] Engler's Bot. Jahrb. Bd. v. p. 401.

[2] Compare our Figs. 2 and 3 with Figs. 1 and 2 in Dr. Scott's memoir.

[3] Quart. Journ. Microscop. Science, vol. xxiv. pp. 196–7.

At the *nodes* the various groups are connected by tangential branches through about half the circumference of the pith, on the side of the stem adjacent to the insertion of the leaf (Fig. 5); the remaining groups are not usually connected by tangential branches. Sometimes however, in moderately young nodes, one finds tubes scattered through the whole of the pith, sending transverse branches in various directions.

Unlike what is the case in certain of the Euphorbiaceae, with non-articulated tubes[1], no branches were observed passing through the medullary rays and connecting the medullary and cortical systems. It appears therefore that there is no communication between these two systems in the internodes.

At the nodes, however, branches of the medullary tubes of the stem pass outwards with the leaf-bundles, and on reaching the cortex branch freely, forming a complicated network, so that it is difficult to distinguish between these vessels and those of the cortical systems. In one case, however, a connection was clearly observed between one of these branches and a tube passing upwards through the phloem of the next internode (Fig. 6). In transverse sections through the same region, radial connections were also observed between members of the various zones of the primary and secondary phloem.

Thus it is probable that at the nodes all the laticiferous systems stand in radial connection with one another[2]. It is interesting to notice the close resemblance between this connection of the medullary vessels with those of the cortex and that in *Euphorbia Lathyris*[3], whose non-articulated tubes differ so widely in their origin from those of *Manihot*. *Jatropha multifida* also has medullary tubes (non-articulated), branches from which were observed passing out with the leaf-

[1] De Bary, l. c., p. 437.

[2] This differs from the arrangement in the internodes, where 'anastomoses in the radial direction were not observed either in the primary or secondary phloem.' Scott in Quart. Journ. Microscop. Science, vol. xxiv. p. 197.

[3] De Bary, l. c., p. 438, Diagram.

bundle. The series of secretory sacs, described by Pax as articulated laticiferous tubes, have also been found to occur in the pith in certain of the Acalyphineae [1].

The pith of the stem and the parenchyma of the upper portion of the petiole are connected by thin-walled unlignified cells elongated in the direction of the leaf-bundle; it seems probable that this tissue is continuous with the groups of 'cambiform' cells occurring immediately outside the pith. The laticiferous tubes passing out to the leaf are usually found in this tissue [2].

Behind the leaf-scar, bordering on the pith and protruding considerably into it, is a mass of lignified tissue, whose elements resemble, in form and arrangement, those of the ordinary pith (Figs. 4 and 6); their walls are however much thickened and pitted. The internal mass of the pith in the internodes and in the older nodes consists of larger cells, which have much thinner walls but are also slightly lignified, while the peripheral portion, as already described, has thin walls of unchanged cellulose.

Transverse sections through young nodes show that the cambium-ring is incomplete behind the leaf-scar (Fig. 5) for some distance above the points where the leaf-bundles join the vascular cylinder of the stem, and that ordinary thin-walled pith-cells occupy, relatively, the same position as do the thick-walled lignified cells above mentioned, in the older stem. These lignified cells cannot, therefore, be a product of the activity of the cambium; they seem to be ordinary pith-cells which have undergone secondary sclerosis. As there is less secondary wood formed behind the leaf-scar than in other parts of the stem, this lignified parenchyma may be needed for mechanical support. The laticiferous vessels pass through it, as through the thin-walled peripheral pith (Figs. 4 and 6).

The mass of the pith in fairly young nodes resembles the outer portion of the pith of the internodes in having thin

[1] Engler's Bot. Jahrb. Bd. v. p. 404.

[2] This tissue is not clearly shown in Fig. 4, which was taken from an old stem.

walls and abundant starch-contents[1]. It is worthy of note that in these young nodes the laticiferous tubes are not, as in the internodes, confined to the peripheral portion of the pith (see above). Their distribution thus shows a relation to that of the starch-containing pith, though, as we have seen, they may also traverse other parts of the tissue.

In older nodes this kind of pith, though forming a thicker layer than in the internodes, does not extend to the centre, which is occupied by large slightly lignified cells, like those forming the internal mass of the pith in the internodes.

It seems probable that some of the inner laticiferous tubes become obliterated by the pressure of these cells in their later growth.

II.

The discovery of nuclei in laticiferous tissue is due to Treub[2], who in 1879 found that the *non-articulated* laticiferous tubes of the plants he investigated (Urticaceae, Asclepiadaceae, Apocyneae, and Euphorbiaceae) were multinucleate. The first to observe nuclei in *articulated* tubes was Dr. Scott[3], who, in describing the laticiferous vessels of *Chelidonium*, mentions that they contain one nucleus to each member of the vessel, and that these nuclei are present as long as the vessel exists.

In the next year (1882) Schmidt[4] described protoplasm and nuclei in the laticiferous *vessels* of several species belonging to Cichoraceae, Campanulaceae, Lobeliaceae, Papayaceae, Papaveraceae, Aroideae and Musaceae. His investigations leave little doubt that throughout these orders the laticiferous vessels retain the essential characters of living elements during their whole existence.

[1] By splitting a piece of the stem down the middle and treating it with iodine solution, the position of the starch-containing pith is very well brought out.

[2] Sur des cellules végétales à plusieurs noyaux in Arch. Néerland. xv. 1880.

[3] Zur Entwickelungsgeschichte der gegliederten Milchröhren der Pflanzen. Diss. Würzburg, 1881. Also in Quart. Journ. Microscop. Science, 1882, p. 152.

[4] Bot. Ztg. 1882, Nos. 27 and 28.

As regards the laticiferous vessels of *Manihot Glaziovii*, nuclei have been already found in the transverse connections by Dr. Scott[1], but the question of their more general occurrence was left open for further investigation. As the euphorbiaceous genera *Manihot* and *Hevea* are the only ones which are known to contain *articulated* laticiferous tubes, not included in the orders investigated by Schmidt, the occurrence of protoplasm and nuclei in the laticiferous vessels of *Manihot* is a point of considerable interest.

By treating longitudinal sections of the stem of *Manihot Glaziovii* with ether and staining with haematoxylin numerous nuclei in the laticiferous vessels both of the phloem and pith were rendered clearly visible.

All the figures refer to the latter system. Figs. 7 and 8 are from a portion of a stem about 2½ millimetres thick at a distance of 15–20 mm. from the apex.

Fig. 9 is from an older portion eight mm. in thickness. The presence of perfectly normal nuclei at this stage of development shows that they persist when the vessels are quite mature[2]. This corresponds with Dr. Scott's observations on *Chelidonium*, and with those of Schmidt on members of the numerous orders investigated by him. The nuclei are seen to resemble those of the surrounding cells in size and structure.

Fig. 9 shows a laticiferous tube passing through the nodal mass of lignified pith, the cells of which have mostly lost their contents. Here also the nuclei in the tube are perfectly distinct.

Alcohol-material being used, the contents of the laticiferous vessels were contracted; they presented a definite outline, such as is described by Schmidt, and their peripheral portion stained deeply with haematoxylin, from which one may infer the presence of a protoplasmic layer.

[1] Quart. Journ. Microscop. Science, 1884.

[2] We also observed that many of the libriform cells of the secondary wood are multinucleate. Dr. Scott mentions the occurrence of multinucleate members in the sieve tubes.

Fig. 1.

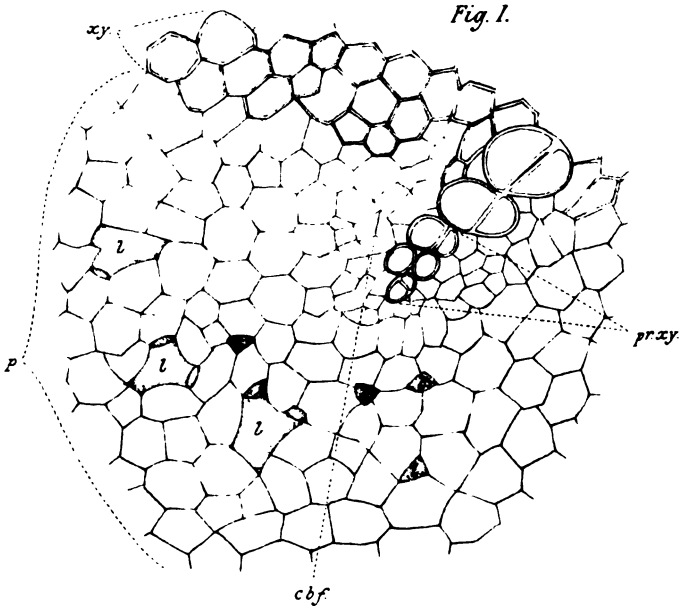


Fig. 4.

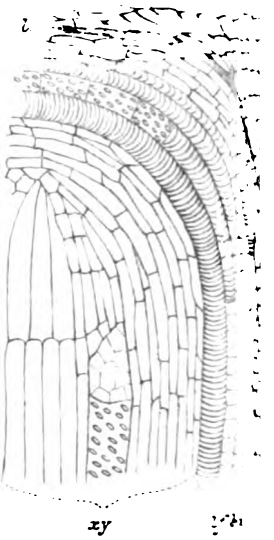


Fig. 2.

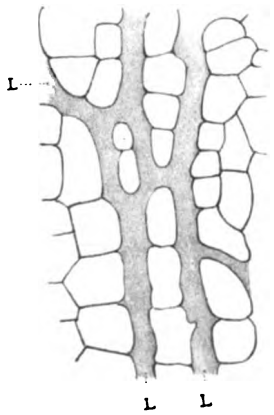
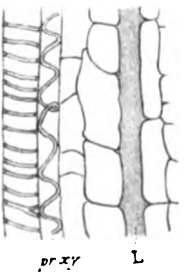


Fig. 3.



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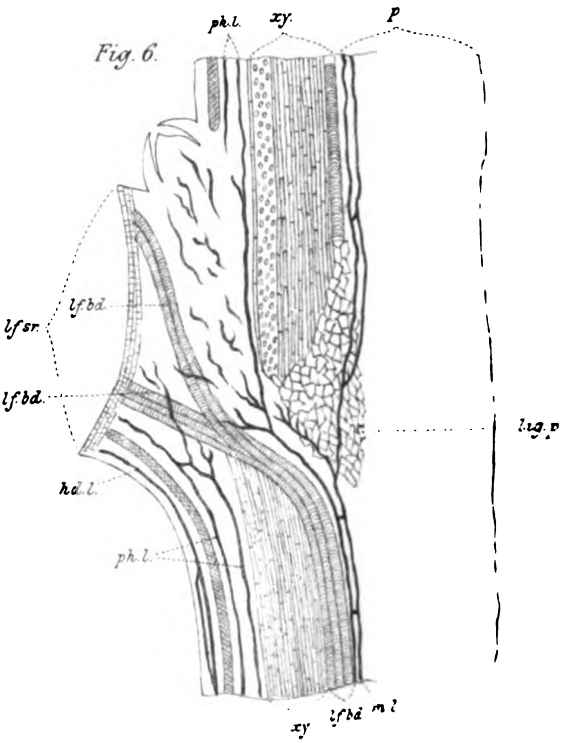

Fig. 5.

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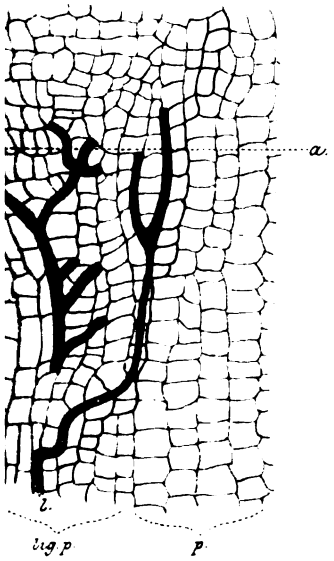


Fig. 5.

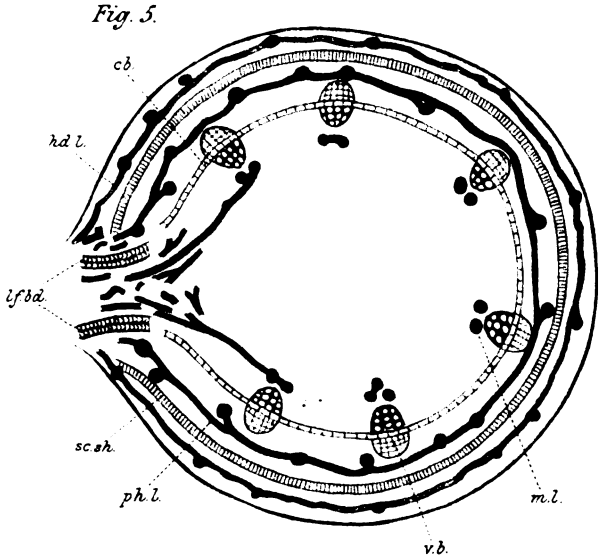
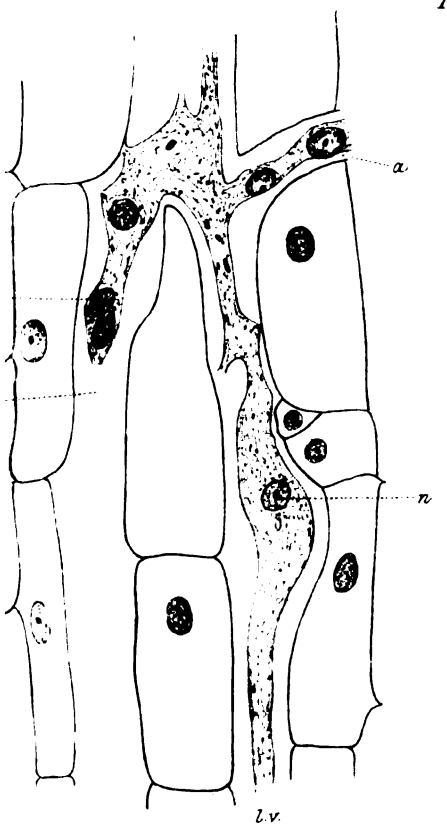


Fig. 8.



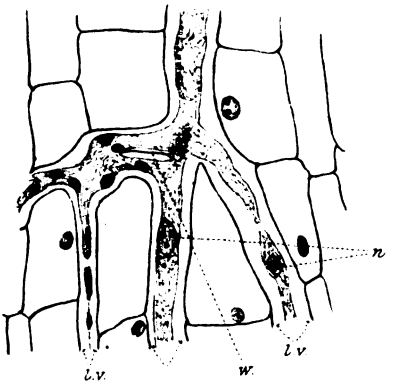
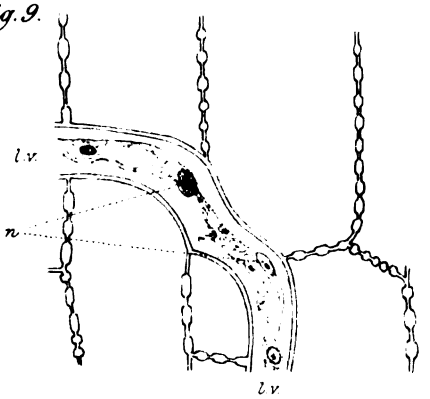


Fig. 9.



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It appears therefore that here, as in other plants with laticiferous vessels, the latter retain their living contents after maturity.

The material for the investigation was kindly supplied from the Royal Gardens, Kew, and the work was almost entirely carried out in the Jodrell Laboratory.

EXPLANATION OF FIGURES IN PLATE V.

Fig. 1. Transverse section through part of a young stem. *pr. xy.* protoxylem. *xy.* xylem. *p.* pith. *l.* laticiferous tubes, three of which branch transversely. *cbf.* 'cambiform.' (× 170.)

Fig. 2. Portions of tangential sections, showing part of a complicated network of medullary laticiferous vessels (*L*) with some of the surrounding pith-cells. (× 150.)

Fig. 3. Portion of a nearly radial section. *L* laticiferous vessel. *pr. xy.* protoxylem. Between the spiral vessel and the laticiferous tube are two layers of pith-cells, the 'cambiform' cells being absent here. (× 150.)

Fig. 4. Longitudinal radial section through part of the node of a stem where secondary thickening has made some progress. *xy.* xylem of part of the stem. *lf. bd.* bundle passing out to leaf. *lig. p.* lignified parenchyma-cells with pitted walls. *p.* ordinary thin-walled pith. *l.* laticiferous vessels. At *a* the tube was not quite distinct, as it dipped below the plane of the section. (× 80.)

Fig. 5. Diagram showing arrangement of the various laticiferous systems in a transverse section of a young node. *lf. bd.* leaf-bundle. *hd. l.* hypodermal laticiferous system. *sc. sh.* sclerenchymatous sheath. *ph. l.* laticiferous system of the primary phloem. *v. b.* vascular bundle. *cb.* interfascicular cambium. *m. l.* medullary laticiferous system.

Fig. 6. Diagram showing arrangement of the laticiferous tissue in a longitudinal radial section through half a node of an older stem. *lf. sr.* leaf scar. *lf. bd.* leaf bundles. *xy.* xylem. *p.* pith. *hd. l.* hypodermal laticiferous system. *ph. l.* laticiferous systems of two phloem-zones. *m. l.* medullary laticiferous system. *lig. p.* lignified parenchymatous cells with pitted walls.

Figs. 7 & 8. Portions of an approximately radial section through the pith of a young internode, after treatment with ether, and staining with haematoxylin. *l. v.* laticiferous vessels: the contracted contents have a definite outline, and several nuclei *n.* are seen. Nuclei are also shown in some of the parenchyma-cells. At *a*,

Fig. 7, there appeared to be a connection with another vessel slightly below the plane of the section. At *w*, Fig. 8, the remains of a partially absorbed wall are seen. (Fig. 7 × 700, Fig. 8 × 350.)

Fig. 9. Part of a radial section through the pith of an older stem, near a node. A laticiferous vessel *l. v.* is shown passing between pith-cells with thick, pitted, lignified walls. The contents have not a continuous definite outline, like that of the other sections, probably owing to difference of treatment. This section was cleared with chloral-hydrate and stained with borax-carmine. (× 700.)

Anomalous thickening in the roots of Cycas Seemanni, Al. Braun.

BY

W. H. GREGG, B.A. (DUBLIN),

Surgeon-Major, Bengal Army.

With Plate VI.

WHILE working in the Jodrell Laboratory, Kew, under the direction of Dr. Scott, and with material which Professor Bower kindly placed at my disposal, I found some abnormal thickening in the roots of *Cycas Seemanni* which does not appear to have been previously observed. Abnormal thickening in the *stems* of *Cycas*, *Dioon*, *Zamia*, and *Encephalartos*, has been well worked out by Mettenius and others [1]. The abnormality consists in the appearance of successively renewed zones of cambium outside the normal ring—each of these in turn continues its activity for a limited period, and then passes over into permanent tissue, while the process of thickening is carried on by a new zone appearing nearer the periphery of the stem. In the case of *Cycas* there is a further abnormal process consisting in the relatively late appearance of distinct cortical bundles—each of which undergoes a certain amount of thickening by means of a cambial ring of its own. As regards the roots of the Cycads our knowledge is far less complete. The researches of Mettenius have made us fully acquainted with the development

[1] G. Mettenius, Beiträge zur Anatomie der Cycadeen, 1860. De Bary, Comparative Anatomy of the Vegetative Organs of the Phanerogams and Ferns, Eng. ed., 1884.

[Annals of Botany, Vol. I. No. I. August 1887.]

of the primary structure, and of the normal products of thickening, in the roots of *Cycas revoluta*, and also in species of *Dioon*, *Encephalartos*, and *Zamia*. The mode of development which he describes essentially agrees with that of the roots of the Conifers; the case of the diarch root of *Cycas revoluta*, which he describes very fully, agreeing for example with such a root as that of *Taxus*. The subsequent occurrence of abnormal growth is mentioned by him in the following words (l. c. pp. 598–9): 'Mit dem höheren Alter der Wurzel erlischt endlich die Thätigkeit der Cambiumschichte, und beginnt gerade wie in dem Stamm ausserhalb des Bastes die Ausbildung einer zweiten, und schreitet das weitere Wachsthum in voller Uebereinstimmung mit dem des Stamm's fort.'

No further details however are furnished on this part of the subject, nor have later investigators, so far as I have been able to ascertain, added anything to our knowledge of the point in question. The writer who in recent times has dealt most fully with the roots of Cycadeae is Reinke; to him is due our knowledge of several points of interest, more especially the curious changes in the roots due to the presence of nostoc-colonies within their tissues; a further observation of special interest was Reinke's discovery[1] of two peridermal layers in *Cycas circinalis*, one derived in the normal manner from the pericambium and the other arising externally at the periphery of the cortex[2]. No observations, however, relating to the abnormal development of secondary wood and bast are recorded by this investigator. In view of the extreme scantiness of our knowledge of anomalous thickening in roots of *Cycas*, the following observations on the roots (preserved in alcohol) of some seedlings of *Cycas Seemanni* grown in the Royal Gardens, Kew, from seed obtained from Fiji, may not be without interest. The material of *Cycas Seemanni*, Al. Braun, which is probably a geographical form of *C. circinalis*, contained five or six good specimens of roots varying in

[1] Reinke, Morphologische Abhandlungen, 1873.

[2] It may be mentioned in passing that I have observed the same condition in the root of *Cycas revoluta*.

thickness from about 15–22 mm. in the thickest portions.

The roots investigated were the tap roots of the seedlings; in the lateral roots no anomalous growth whatever was found. The abnormal thickening was confined to a region from 20–40 mm. in length, measured from the junction of the stem with the root.

In order to understand the phenomena which I am about to describe, it will be necessary first to give an account of the structure of the roots in question, before the abnormal development made its appearance. This was easily ascertained by making a series of sections from the younger portion of the root. I found that the very young portions had usually the ordinary diarch arrangement of the bundles; one case of a triarch root was observed. The primary structure need not be described in minute detail, as it agrees in the main with that recorded by Mettenius. The primary groups of the diarch xylem unite to form a median plate, the elements of which become to some extent separated from one another by the greater growth of the conjunctive parenchyma. The primary phloem-groups have the usual position on the right and left of the primary xylem-plate. The normal cambium arises along the inner side of these phloem-groups, and produces in the usual manner two masses of secondary xylem on the side towards the primary plate, while on the outside secondary phloem is produced. Except in one case, to be described later on, the normal cambial layer was not found to become continuous around the ends of the primary xylem. The pericambium was many layers of cells in thickness, as is usual in Gymnosperms, and it is owing to this fact that the abnormality to be presently described is possible. The pericambium is surrounded by a well-marked endodermis of the usual character. This is again surrounded by a wide cortex. The structure of the root at the stage which we are now considering may well be compared with the root of *Taxus* as figured by Strasburger[1]. It may here be mentioned

[1] Das botanische Practicum, p. 201.

that the roots investigated retained their cortex, even in their oldest portions, only external periderm being formed (see De Bary, l. c. p. 613). The anomalous development consists essentially in the formation of additional cambial layers external to the normal one; the process as observed appears under two modifications, one of which was only found in a single root, while the other occurred in all the remaining roots examined. The latter will be first described. In this case the abnormal development begins by the formation of cambial divisions in cells of the pericambium lying at a short distance from the ends of the normal cambial layer[1]. Other divisions soon begin both in the cells lying immediately outside the normal phloem, and in those immediately adjacent to the ends of the normal cambium; so that ultimately a complete cambial ring is formed, consisting on its inner side of the original normal cambium, and on its outer side of the more recently formed layer—it will of course be understood that as this process goes on on both sides of the root, two complete rings of cambium are formed. The anomalous portion of each of these rings produces numerous layers of xylem on its *outer side* and a considerable amount of phloem towards the interior. In this reversed orientation of the products of the first developed anomalous cambium, lies the most characteristic peculiarity of the structures we are considering. As a result of this reversed orientation the tissue lying between the anomalous and the normal cambium becomes compressed (see Figures).

At a somewhat later stage a second process of abnormal development begins; this process, like the one last described, takes its rise from the pericambial tissue. In the cases where the very first origin of this was observed, the development began by divisions in the outermost layer of the pericambium lying immediately below the endodermis as shown in Fig. 2, and it is thus separated by numerous layers of cells from the

[1] See description of Figures.

secondary products already considered; these divisions first make their appearance in scattered cells in the layer in question, the exact position of which appears to be indeterminate, with the limitation that the process was never found to begin at the points opposite the primary xylem-groups. The divisions thus started eventually extend to the intervening cells, so as to form a single complete ring of cambium, extending around the vascular cylinder of the root without any interruption, even opposite the primary groups of xylem. This outer cambial layer thus arises in the position usually occupied by the phellogen of the roots; here, however, its character is that of a true cambium, and it produces numerous xylem-elements on its inner side, and hard and soft bast on its exterior; thus as regards their orientation the tissues produced of this layer are normal. As would be expected from the fleshy character of the root as a whole, the xylem produced does not consist entirely of lignified elements, but includes a number of thin-walled parenchymatous cells scattered among the tracheides.

The general structure of the root at a relatively advanced stage is illustrated by Fig. 3.

It may be mentioned that in one root belonging to the type first described the original arrangement of the bundle was triarch instead of diarch; here the phenomena of secondary thickening both normal and abnormal went on, *mutatis mutandis*, precisely in the same way as in the diarch examples, the resulting structure simply showing three inner rings instead of two.

As regards the second form of thickening I have referred to, the primary structure of the root in question was identical with that of the diarch root first described, and the normal secondary thickening also begins in the same way; here however the normal cambium-layer extends around the ends of the primary xylem-plate so as to form a single complete ring[1]. Before this ring is complete the first anomalous cam-

[1] As in the case described by Mettenius, l. c. p. 597.

bium makes its appearance as above described, but it never becomes continuous with the normal cambium. The orientation of its products is here also reversed as compared with the typical arrangement. The activity of this cambial layer results in the first instance in the production of two isolated bands of secondary tissue lying on either side of the normal vascular mass; subsequently a new series of divisions begins at the outer limit of the pericambium corresponding to those producing the outermost secondary ring in the first type; the products of these divisions resemble those in type 1; the outer cambial layer, however, never forms a complete ring round the whole vascular cylinder, but on the other hand becomes continuous on either side with the first anomalous cambial layer (see Fig. 4). If we take only diarch roots into consideration, the differences between the two types may be summed up as follows:—In Type 1 we get two inner rings of secondary tissue surrounded collectively by a single outer ring; in Type 2 we get a single internal ring flanked on two sides by two anomalous outer rings. As follows from the mode of development described, the outer rings in Type 2 have the opposite arrangement of the xylem and phloem to that in the inner rings of Type 1[1]. It is a point of some interest that all the cambial layers observed appear to continue their activity simultaneously. Judging from the relative thickness of the cell-walls, there is no reason to suppose that the inner cambial layers pass over into permanent tissue when the outer ones begin their activity; how long this simultaneous growth of all the layers may continue could not of course be determined in the material available. As regards the nature of the xylem and phloem-elements derived from the inner and outer abnormal cambium, no important differences were found as compared with the normal secondary tissue.

It is important to mention that the peculiarities of structure described in these roots have no relation to any abnormality

[1] The structure of the rings in question may be compared to that of concentric bundles.

Fig. 1.

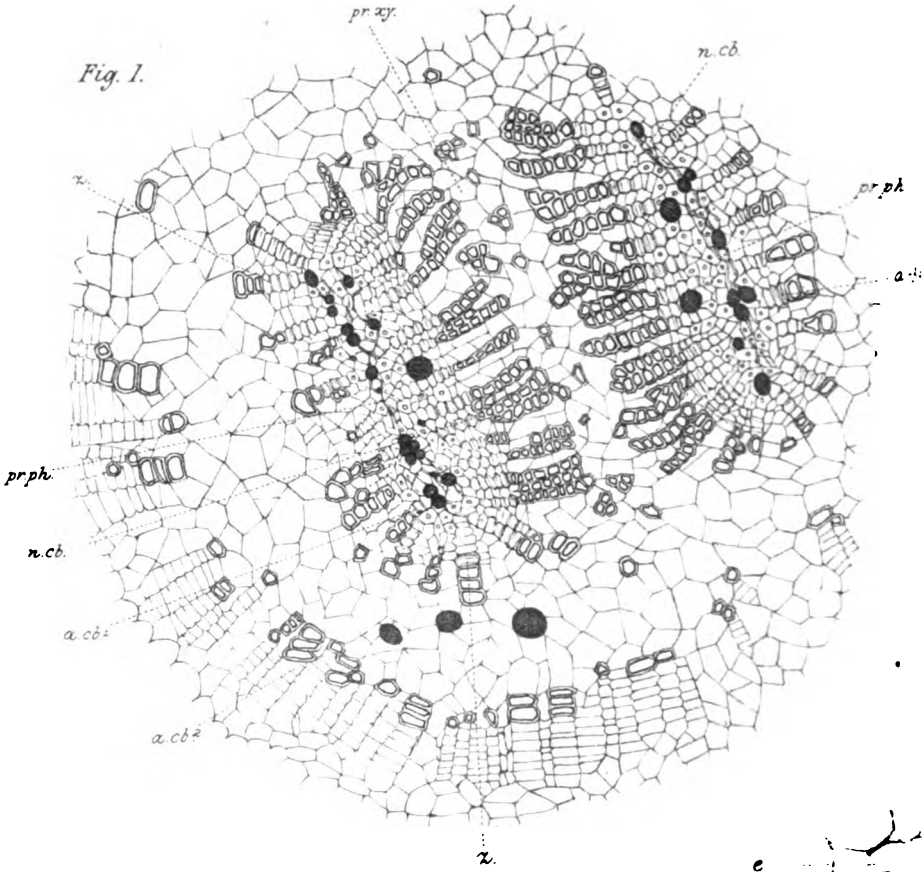
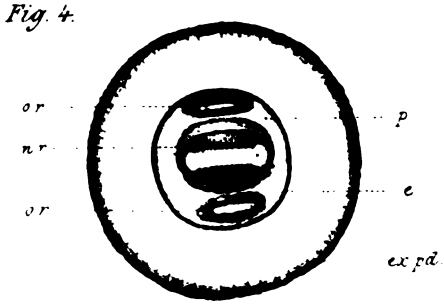


Fig. 4.



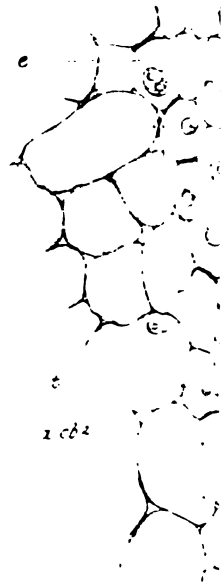


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Fig. 3.

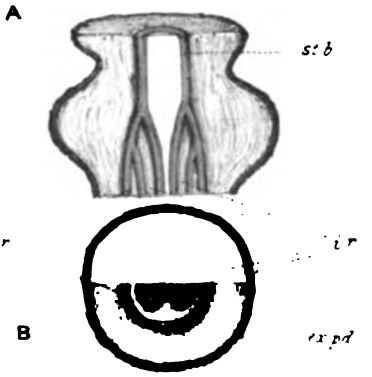

Fig. 2

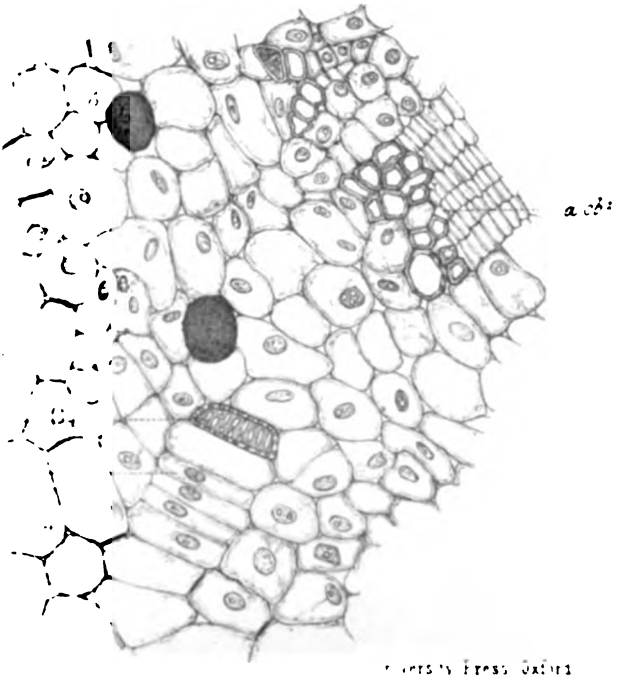

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Fig. 1

in the stem. In all the seedlings investigated the stem showed simply a normal ring of collateral bundles without any abnormalities of thickening whatever. At the transition from root to stem the anomalous zones of the root abut on the bundles of the stem, in the way indicated in Fig. 3.

In conclusion, the general results of the investigation may be summed up as follows:—

1. All the anomalous thickening observed proceeds from cells of the many-layered pericambium.

2. The first anomalous cambium arises in the inner portions of this zone.

3. The second anomalous development starts from the extreme outside of the pericambium.

4. The orientation of the inner anomalous tissues is reversed, the phloem lying towards the centre, the xylem towards the periphery of the root.

5. In the outer anomalous region the orientation is normal.

That further processes of abnormal development may occur in the older root is extremely probable, but this can only be determined by the examination of more advanced specimens than those at my disposal.

EXPLANATION OF FIGURES IN PLATE VI.

Fig. 1. Transverse section of a root of type 1, showing a portion of the vascular cylinder only. *pr. xy.* primary xylem plate. *pr. ph.* compressed remains of primary phloem. *n. cb.* normal cambium. *a. cb.*$_1$ first abnormal cambium, its products have reversed orientation. *a. cb.*$_2$ second abnormal cambium. *z.* approximate starting points for the development of the first abnormal cambium. The cells shaded black contain tannin. (× about 45.)

Fig. 2. Portion of a transverse section of a younger root of type 1, showing the origin of the second abnormal cambium. The first abnormal cambium has already produced numerous permanent elements. *e.* endodermis. *a. cb.*$_2$ second abnormal cambium. *t.* tracheid already derived from it. *a. cb.*$_1$ first abnormal cambium. (× 140.)

Fig. 3. A. Longitudinal section of the junction between stem and root in type 1. B. Transverse section through the root of the same. *c. o. r.* common outer ring.

i. r. inner rings, in each of which the half towards the centre of the root has been derived from the normal, the half towards the periphery from the first abnormal cambium. *ex. pd.* external periderm. *st. b.* normal ring of bundles in the stem. (× 2.)

Fig. 4. Transverse section of a root of type 2. *n. r.* normal ring. *o. r.* abnormal outer rings. *e.* endodermis. *p.* pericambium. *ex. pd.* external periderm. (× 4.)

In Figs. 3 and 4, the xylem is coloured yellow, the phloem blue, and the periderm brown.

NOTES.

PHENOMENON ANALOGOUS TO LEAF-FALL.—In the text-books of plant-anatomy it will be found mentioned[1] that in some species of *Rubus*—as also in *Ribes*, *Lonicera*, etc.—the cork-forming meristem or phellogen arises in the inmost layer of the primary cortex, or at the external limit of the bast-fibres (*stereom*). In this note I wish to call attention to the case of *Rubus australis*. This species is rendered interesting from its peculiar habit, and from the rudimentary condition of its leaves: these latter are characterised by possessing no lamina—they consist simply of the midribs of the single unpaired and of the paired leaflets of the compound leaves commonly found in members of the genus. These midribs are thickly beset with prickles, with points directed downwards. Such a disposition of the prickles is also characteristically found in other Rubi; but here their development is much more strongly pronounced, so that they constitute a most formidable climbing apparatus, which has very obviously been derived from the commonly occurring *Rubus*-type. The younger shoots are of a deep green colour, and their importance in the total assimilative activity of the plant is a considerable one, the leaves being in so reduced a condition. A tranverse section of a young first-year's shoot shows the ordinary ring of primary vascular bundles, with more or less secondary xylem and phloem according to its age. Immediately outside the ring of bundles is a broken ring of bast-fibres (*stereom*), each fascicle of such fibres being immediately outside a primary phloem. The gaps in this stereom correspond to the points where the primary medullary rays run into the cortex. The cortex consists of some ten to a dozen layers of parenchymatous cells, all of which are assimilative, bounded externally by the epidermis. The two or three outermost layers are not quite so richly assimilative as the more deeply lying ones, as estimated by the number of corpuscles in each cell. Towards the end of the summer a phellogen is developed. This is formed from the inmost of the assimilating cortical layers—

[1] Cf. De Bary, Comp. Anat., Eng. edit. p. 552.

immediately external to the stereom-sheath—and therefore removed some ten or twelve layers from the epidermis. By its activity several layers of cork are formed and the cortex is thus cut off from the other tissues, and during the second year is cast off in scales. It is this throwing off of the assimilating cortex in a plant in which the stem is the chief assimilatory part that presents such a curious analogy to the ordinary fall of the leaf in leaf-possessing plants. Just as in these, leaves of one year are functionally replaced in the succeeding year (in deciduous plants) by leaves borne on shoots of the same year's development, so in such a plant as *Rubus australis* the assimilative tissue of one year, i.e. the *cortex* of the shoots of that year, is replaced in the next by the cortex of the shoots of the current year, and the last year's cortex is cast off from the plant by the development of a periderm.

Of course a similar state of things must occur, differing only in degree from this, in all cases in which a cork-cambium is formed inside any cortical layers, which assimilate even to a very small extent; hence my comparison of this cortical shedding to leaf-fall may be considered a forced one.

It seems to me, however, that such a contrast is justified—the agent in either case being the same, and the parts removed, though differing in morphological value, are physiologically identical.

A good example of the same thing is found in *Casuarina*[1]. Here the stem-internodes have longitudinally-running ridges separated by deep grooves. These ridges are constituted almost entirely of radially elongated chlorophyll-containing cells. These form the chief assimilative tissue of the plant. Here also, as in the previously described case, there is a throwing off of this tissue. Periderm first makes its appearance in the *grooves*, and is formed here from the sub-dermal layer of cells. It is gradually continued across the tissue intervening between one groove and another, so that the ridges are completely cut off and by the second year begin to scale off. The resulting phellogen approximates in transverse section to a circle; in the grooves the epidermis is the only primary tissue cut off by it, but between the grooves several layers of palisade-cells are removed in addition to the epidermis.

F. W. OLIVER, Kew.

[1] Vide De bary, Comp. Anat., Eng. edit., p. 553. Also H. Ross, Berichte d. deut. bot. Ges., 1886, p. 367.

THE TRANSPIRATION OF THE SPOROPHORE OF THE MUSCI.—In the account of the anatomy of the sporophore of Mosses which I have given elsewhere[1], a thin-walled strand of tissue (which I have named *leptoxylem*) in the centre of the '*central strand*' is assumed, on anatomical grounds, to be that which conducts the transpiration-current up the seta to the apophysis, the organ of absorption and assimilation of gases and of *transpiration*.

Recently I obtained material very suitable for testing by direct experiment whether indeed this *leptoxylem* does, or does not, conduct the transpiration-current.

To do this I found that the best method was to make experiments with two different species of Moss; in one of them the tissues were well differentiated, and in consequence rather large and opaque; the other I chose on account of the transparency of its tissues, so that the transpiration-current could be observed without mutilating the tissues. The Mosses used were *Polytrichum formosum*, Hedw., and *Splachnum sphaericum*, Linn. The method adopted was that of placing the cut ends of the sporogonium in a drop of eosin.

In the case of *P. formosum*, after a short time, about 30 minutes, on splitting up the seta and extracting the central strand and examining it, it was found that the eosin had penetrated up the central part of the central strand only. But this did not show exactly into what tissues the eosin went; therefore, a transverse section of another seta was made which had been treated similarly to the first, and this showed clearly that the eosin passed up the seta by means of the leptoxylem, although, as was only to be expected, the eosin, after some considerable time, penetrated into other tissues. The rate of transpiration could not be observed with any accuracy in *P. formosum* on account of the opaqueness of its tissues.

In *Splachnum sphaericum* the rate of transpiration could, on account of the transparency of the seta, be observed with the greatest ease, the current going up the centre of the seta only; but on account of the extreme delicacy of the tissues the exact limits of the tissue which conducted the transpiration-current could not be determined.

Watching measured distances of 2 mm. along a part of a seta, the eosin could be seen to move over the measured space in 2 minutes.

[1] Vaizey, On the Anatomy and Development of the Sporophore of the Musci (Part 1, Polytrichaceae). Journ. Linn. Soc.

This was observed again and again on different setae. On a long seta a distance of 30 mm. was measured, the ends of the course being marked; the eosin passed the first mark at 10.47 a.m., and the second at 11.31 a.m., thus taking 44 minutes to do the whole distance, which is a slower rate than that recorded over the short distances. This is, I think, accounted for by the facts, that in the long distance there were one or two twists in the seta, and the measurement was taken in a straight line, so that my account should rather under than overstate the case, that in watching the short distances there must be some unavoidable errors of observation, and also that there must be a good deal of variation between individual setae. I frequently observed the eosin pass up the whole of the seta and enter the apophysis, which was found by means of transverse sections to have a quantity of eosin in its centre. These experiments sufficiently confirm, I think, my original view, based on anatomical grounds, as to the function of leptoxylem.

I have, in conclusion, to thank Mr. P. Ewing, of Glasgow, for sending very fine living specimens of *Splachnum sphaericum*, and thus enabling me to carry out these experiments.

J. REYNOLDS VAIZEY, Cambridge.

THE PRICKLE-PORES OF VICTORIA REGIA.—On page 54 of De Bary's Comparative Anatomy of the Phanerogams and Ferns (English Edition) the following passage occurs:—

'The openings which Trécul describes on the large prickles on the leaf-nerves and petioles of *Victoria regia* may be here supplementarily mentioned, being doubtful as regards their structure, and requiring further investigation. These prickles enclose a thin vascular bundle, which ends under their apex, and at the apex is to be found a depression with one circular opening (ostiole).'

The results of further investigations are as follows:—

(1) Fibrovascular bundles only occur invariably in the largest spines, rarely in those less than one inch in length, and then the elements are fewer and but slightly lignified.

(2) The spines themselves either taper to a finer point than in Trécul's figure, being composed of two or three cells only at the extreme end, or they are variously truncated. The ostioles and depressions could not be seen either in surface-views of the ends or in longitudinal sections through the apex.

(3) The apices of the spines are lignified, and the lignification

extends about three-fourths of the way to the base, giving the spines a glistening appearance. The cells with lignified walls form a solid cap at the apex; below they are confined more and more to the superficial layers, forming altogether a hollow cone, thinning out towards the base. There is no trace of any 'epithema.'

Trécul's figures of the ostioles strongly resemble the perforations of the leaves, which he states are due to insects. This, coupled with the fact that they do not occur constantly, points to the opening being pathological. The function of the spines is therefore probably only protective, the fibrovascular bundles, as in other emergences, being only present in the larger ones. The distribution of the spines shows that they must be for protection against some submerged animal of a fairly large size.

J. H. BLAKE, Cambridge.

THE LATICIFEROUS TISSUE IN THE STEM OF HEVEA BRASILIENSIS.—The material used in this investigation formed part of some supplied by Dr. Trimen, from Ceylon, and consisted mainly of seedlings 21 to 25 days after their appearance above ground. Sections of younger seedlings were also examined.

The work has been done under the advice and direction of Dr. Scott, and has been carried out in the Jodrell Laboratory, Kew.

Distribution of the Laticiferous Tissue. In the hypocotyledonary and epicotyledonary stems of the younger seedlings laticiferous tissue is abundantly developed in the *inner cortex*[1], but none was observed either in the outer cortex or in the pith. In older seedlings, however, *medullary laticiferous tubes* occur in the upper part of the first epicotyledonary internode, and in the succeeding internodes[2].

In most cases the medullary tubes seem to be connected with those of the cortex only at the node, but in one case a tube was distinctly seen running obliquely upwards from the cortex, passing between the vascular elements and continuing its course in the pith. This occurred at a short distance below the node.

[1] Cf. Scott, On the Laticiferous Tissue in *H. spruceana*, in Quart. Journ. Microscop. Sci., vol. xxiv. p. 206. Also in Journ. Linn. Soc. (Botany), vol. xxi. 1885, p. 566.

[2] The first internode of the epicotyl in these seedlings measured 9–10 inches in length, and medullary laticiferous tubes were only found in the upper half-inch. The second internode in no case reached half-an-inch in length.

In two other cases medullary tubes seemed to come directly from the vascular ring, but they had been cut across and could not be traced between its elements.

Connections between the medullary and cortical laticiferous tubes may occur in young internodes, and may be obliterated as secondary thickening proceeds. Older seedlings would be required to determine this.

In the *hypoderm* or *outer cortex* of the upper part of the stems of the older seedlings laticiferous tubes also occur[1]. They seem to arise as branches from the *main* system of tubes in the inner cortex. Branches from these tubes are frequently found running obliquely upwards through the cortex, passing between the elements of the sclerenchymatous sheath, and continuing their course in the hypodermal tissue.

In *Manihot Glaziovii* no connections between the hypodermal and cortical systems were observed except at the nodes, but *seedling* plants were not examined. Probably the two systems may be quite as distinct in the internodes of mature plants of *Hevea brasiliensis*. The condition of the laticiferous tissue at the nodes closely resembles that in *Manihot*, the sclerenchymatous sheath being interrupted, and the abundant and irregular branching making it difficult to distinguish between the two systems. Hypodermal laticiferous tubes were only found in the upper half-inch of the first internode of the epicotyl and in the succeeding short internodes.

Blind endings. The ultimate ramifications of the laticiferous tubes of the hypodermal and medullary systems frequently become very narrow and appear to terminate blindly. Similar endings are found among the tubes of the inner cortex. They are, however, of rare occurrence except in the neighbourhood of a node.

It appears, therefore, that though the laticiferous tubes in this plant consist mainly of vessels formed by the fusion of rows of cells[2], yet these vessels, like the laticiferous *cells* of other euphorbiaceous plants, retain the power of independent growth, and may put out branches which grow by their apices.

Reticulate anastomoses occur both in the hypodermal[3] and medullary systems, but are of much less frequent occurrence than in the tubes of the inner cortex.

[1] Cf. Scott, loc. cit. [2] Scott, loc. cit. [3] Scott, loc. cit.

Nuclei and Protoplasm. In the laticiferous tubes of all three systems the nuclei are particularly large and distinct. They are readily distinguishable even in unstained sections. Staining with hæmatoxylin or with methyl-green brings them out very clearly. They are large and granular, and closely resemble those of the surrounding cells. They frequently contain very distinct nucleoli.

When a tube narrows considerably and then ends blindly a nucleus is frequently found just below the point where the narrowing takes place. Where the latex has contracted from the walls of the tubes, the protoplasmic layer may be seen, giving a sharp, definite outline to the contracted contents. It is much more definite than is the case in *Manihot Glaziovii*.

Possibly the abundance of the protoplasm and the size of the nuclei may be correlated with the independent growth of the tubes, above referred to. In some cases several nuclei were found very close together in a tube, but no division stages were observed.

The latex is coarsely granular in mature tubes, much more finely granular in the younger parts. It is clearer in the tubes at a node than in those in an internode, hence sections near a node are most suitable for the study of the nuclei.

AGNES CALVERT, London.

'SPOROPHORE' AND 'SPOROPHYTE.'—Into the English edition of Goebel's Outlines of Comparative Morphology and Classification of Plants I imported the word 'sporophyte' with the concurrent 'oophyte' as equivalents for 'asexual generation' and 'sexual generation' respectively in Vascular Cryptogams. 'Sporophore' and 'oophore,' which were used by Vines in the second English edition of Sachs's Text-book, as terms for these generations, are quoted in Goebel's Outlines, but preference is given to 'sporophyte' and 'oophyte.' The necessity for this modification in the terminology has been questioned by several critics in reviews of the edition of Goebel's work, and rightly too upon the evidence, for no explanation of the change was offered. But the innovation was made only after full consideration, and in view of the use of the term 'sporophore' with another signification in the English edition of De Bary's Morphology and Biology of the Fungi, Mycetozoa, and Bacteria, which has just been published; and I now take the opportunity of giving an account of the reasons which led to the introduction of the terms in question, terms for

which (at least for one of them—'sporophyte'), with the meaning attached to them in Goebel's Outlines, De Bary is primarily responsible.

The term 'sporophore,' or rather a latinised form, 'sporophorum,' appears to have been first used by Link in the sense in which we now employ 'placenta' in speaking of Phanerogams, but in this sense, like several other terms for the same structure, never came into general use.

In 1839 Berkeley used the term in the form of 'sporophori' for the structures in Fungi, which, as it turned out, Leveillé had shortly before designated 'basidia,' by which term they are now usually known, distinguishing in this way structures in which spores are exogenetic, from 'sporidia,' structures producing endogenetic spores, and which we now usually speak of as 'asci.' His terminology is consistently followed out in the works of the veteran English Mycologist.

The first employment of 'sporophore' and 'oophore' as the equivalents of 'asexual generation' and 'sexual generation' with which I am acquainted is in the article 'Vegetable Biology,' by Thiselton Dyer, in the new edition of the Encyclopædia Britannica, and there no previous authority is assigned for the use of the terms with this signification. The adaptation of the words was in many ways a very convenient one, for some such expressive terms were wanted, and in oral teaching in Britain they have been widely adopted, although it is only within the last few years that they have crept into teaching-books. As preceding uses of 'sporophore' had not become general, there was no real objection to Thiselton Dyer's terminology, and I should probably not have suggested any alteration but for a difficulty which cropped up in the preparation of the English edition of De Bary's Comparative Morphology and Biology of Fungi, Mycetozoa, and Bacteria.

The difficulty was the following. It was necessary to find an English equivalent for the German 'Fruchtträger,' as used by De Bary in his book in the sense of any structure having spores. 'Carpophore,' the literal rendering, and other compounds of *καρπός*, as well as 'fructification' and 'fruit,' were impossible because they are reserved properly for structures which are the product of the sexual act, and in that way do not cover the ground included in 'Fruchtträger,' and moreover 'fructification' in this proper sense is used in the volume. The general term 'receptacle,' which has been elsewhere employed to translate 'Fruchtträger,' has already so many special meanings attached to it, that it would have been misleading and unwise to make use of it.

After much consideration and consultation with friends, I could find no better solution of the difficulty than to extend the signification of 'sporophore,' as used by Berkeley, beyond the special structures to which he restricted it and to include under it all structures which bear spores of any kind, thus making it the equivalent of 'Fruchtträger.' With this meaning 'sporophore' is consistently applied in De Bary's book, and with satisfactory results so far as my own judgment serves me; I have not yet seen a critical review. Justification of this employment of the word, notwithstanding the other signification given to it by Thiselton Dyer, is to be found in the fact that my interpretation is merely an extension of an older meaning than that given it by Thiselton Dyer, and that in his sense the word has not yet come into general written use.

I may also note that Sprengel had already used the adjectival form 'sporophori' in speaking of the asci of lichens as 'asci sporophori,' so that the term has been in this way applied to structures amongst Fungi which produce spores endogenetically as well as exogenetically, although it was to the latter only that Berkeley restricted it.

Having thus assumed 'sporophore' as the equivalent of 'Fruchtträger,' it was necessary to find a word to express 'asexual generation.' Probably had it been necessary to coin a new word, I should have hesitated in making the modification indicated, but a word ready to hand existed in 'sporophyte,' which readers of De Bary's book on Fungi will find explained there. In the interesting introduction in that book to the second part of the division upon Fungi, 'spore,' 'sporocarp,' 'sporophyte,' are used as terms for three stages in complexity and relative independence of the product of the sexual act; 'spore,' describing the condition in *Spirogyra*, *Mucor*, etc.; 'sporocarp,' fitting the phenomena in the higher Thallophytes and Muscineæ; whilst in Vascular Cryptogams and higher forms we come to the 'sporophyte.' I had merely to add the corresponding 'oophyte.'

Objections to 'sporophyte' in the sense of 'asexual generation' may of course be urged: its use for instance by some authors for the whole group of Cryptogams as distinct from Spermaphytes, the Phanerogams. But I do not require to discuss this further question here, as I only adopted a term already in use for the thing designated. At the same time, to this specific objection I would answer that I do not recognise the necessity for changing terminology merely because a term in use happens to be less expressive of an actual fact than could

be devised, and that the older terms Cryptogam and Phanerogam are in my view quite adequate, and intrinsically are no more objectionable than 'Sporophyta' and 'Spermaphyta,' one of which certainly implies erroneous doctrine.

For similar reasons I need not refer to the many other terms which have been proposed by authors as more satisfactory than compounds with 'sporo' and 'oo' for 'asexual generation' and 'sexual generation.' In a completely reformed terminology more literally expressive words might doubtless be secured. I am concerned here only in explaining the grounds upon which a departure was made from the terminology 'sporophore' and 'oophore' in Thiselton Dyer's sense which appeared likely to come rapidly into general use in Britain.

ISAAC BAYLEY BALFOUR, Oxford.

REVIEW.

LECTURES ON THE PHYSIOLOGY OF PLANTS by JULIUS VON SACHS. Translated by H. MARSHALL WARD. Clarendon Press, Oxford, 1887. 836 pp., 455 woodcuts.

THE days of hack-translators,—at least as far as science is concerned,—are, we trust, numbered. Every one now-a-days expects that a scientific book shall be translated by some one conversant with its subject-matter. In this respect Professor Sachs's latest book is fortunate, and in welcoming the translation we must record our satisfaction at seeing the name of Professor Marshall Ward on the title-page as that of the translator. He has done his work solidly and well, and has produced a readable and trustworthy English version. And if here and there a Germanism remains, we must remember how penetrating and insidious an essence this same Germanism is, how it lurks in the simplest phrases, hiding in the crannies between the words, whence nothing short of ruthless demolition of the original construction will completely remove its traces. The book has been well got up by the Clarendon Press, the only criticism that we have to make being a gentle complaint against the similarity in its outward garb to that of the 'Text-Book.' In this matter we have long ago learned to appreciate the wisdom of bees who, as Hermann Müller has shown, insist on closely allied flowers being distinguished by differences in colour, so that they may not lose time in mistaking one for the other.

No one with a knowledge of what Professor Sachs has done in Botany can be otherwise than grateful for the powerful influence which his teaching has had on the progress of the science. In the forefront of those who owe him a debt of thanks, we place ourselves. And we give emphatic expression to our recognition of his great services whether in teaching or research, lest in our criticism of this his latest book our lasting admiration of what he has done should be forgotten.

The motives which induced the author to undertake the present

volume are given in the preface. Not only was the idea of working up a fifth edition of the 'Text-Book' repellent, but he found that the form of that work had become unsuitable to the views that had gradually taken shape in his mind. He wished, moreover, to appeal not merely to students, but to a wider circle of readers. He was thus led to adopt the freer form of exposition attainable in a series of lectures. Professor Sachs is well known to be a master in the art of lecturing, but we believe this volume will add to his reputation as a teacher. Having suffered somewhat in our day from our teachers, we have only to fix our minds intently on some of these bygone experiences, to be able to call up, in complementary colours, an image of what a lecture ought to be.

We rejoice at being able to recognise some of the best characteristics of a lecturer in our author. He has that most important quality, the power of impressing his readers with his deep and absorbing interest in the subject. He knows when to be brief, and when to enter into details. Fortunately too he speaks out of the fulness of knowledge—a circumstance which gives an ease and solidity to his manner of handling his facts, which in some indefinable way makes itself felt by all classes of readers. There is however occasionally noticeable a certain tone of what we will not call egoism, but rather a sensitiveness with regard to his own contributions to science, which we would gladly find absent in a lecturer, and it is a blemish which we do not remember in his earlier books, for instance in the *Experimental Physiologie.*

Another quality, most excellent in a lecturer, we find in Professor Sachs,—namely, an artistic temperament. To him the manner of presentment is a point of great moment. The arrangement of his facts and arguments is evidently a labour of love over which he spares no pains; with the result of producing a rounded well-balanced whole, clad moreover in a style and language appropriate to so strong and vivid a thinker. He points out[1] that it is the duty of a lecturer to 'place in the foreground his own mode of viewing the matter; the audience wish to know and should know how the science as a whole shapes itself in the mind of the lecturer, and it is comparatively unimportant whether others think the same

[1] Preface, p. v.

or otherwise.' It is from this point of view that he wishes to be criticised, a wish that we shall not fail to bear in mind, in spite of the difficulties which it adds to our task.

The book is a treatise on Physiology, and the author's treatment of his subject is eminently, we had almost said superabundantly, physiological in tone. He seems to have felt the weariness and dryness of the older morphological work, for he writes (p. 2), 'the formal morphological contemplation of the organs of the plant customary hitherto, has left their physiological relations entirely out of account.' We shall be among the first to accept a manner of teaching Botany in which as far as possible physiological conceptions are not neglected, yet we cannot but think that in his objection to the elder morphology Professor Sachs takes up an exaggerated attitude, and that he has neglected a possible position, which might have been equally serviceable for purposes of exposition, and perhaps more logical in itself. The volume begins with a lecture, on 'physiological organography,' in which a standpoint is developed on which we have some remarks to make. The following passages give the pith of the matter (p. 2). After pointing out that it is not possible 'to express organographical ideas clearly and exhaustively by means of simple definitions,' he goes on :—

'We adopt, therefore, a totally different mode of consideration. Without concerning ourselves in any way with definitions, we regard first the various organs where they present themselves in the highest perfection in their typical characters and then seek to establish which organs, in other regions of the vegetable kingdom, present also the same peculiarities more or less modified. In doing this, however, we place in the foreground the physiological properties which very often correspond but little with the relations of outward form which constitute the subject-matter of morphology. I believe, however, that this comparative physiological method of consideration of the organs apprehends their true nature in a more fundamental manner than morphology has hitherto done.'

Here we have organography regulated by the idea of a type. Now it is the essential characteristic of morphology (distinguishing it from organography pure and simple) that a type is ever before the eyes of the describer. But it is a type distinguished by form, whereas in Professor Sachs's physiological organography the type is an abstraction of physiological qualities. In the morphology of our fathers the type kept in view was believed to correspond to the plan on which creation had proceeded, a point of view necessarily unfruitful since it is incapable of development; but morphology standing on the basis of

evolution is a different matter. It is, as Darwin has said[1], 'the most interesting department of natural science, and may be said to be its very soul.' But this is only true of evolutional morphology, which sees in unity of type the expression of community of descent, and thus throws into the study of form that vitality which before it lacked. A similar change has been wrought by evolution on teleology. The belief that each organ was formed in its present shape by the Creator for a certain purpose has no doubt had a stimulative effect on the study of function. Nevertheless the fact remains that the investigation of the uses of the parts of living things only sprang into its present youthful vigour when the 'Origin of Species' had rendered possible a new and vivid science of evolutional teleology. Thus, these two branches of inquiry, morphology and teleology, which had no other bond than such as could be gained by guesses at the will of the Creator, are now connected on the basis of the theory of 'evolution by means of natural selection.' We have dwelt on those considerations because we think that morphology, as it now exists, 'wedded' as Professor Asa Gray has said 'to Teleology,' is a science capable of embracing physiological considerations; and because we believe that it is not necessary for the physiologist to rebel against the usages of morphology in his search for a striking standpoint.

In reading the first lecture we find ourselves forced to ask in what way Professor Sachs arrives at his physiological types. A morphological type connects itself with the theory of descent, but on what basis can Sachs's types stand? An example will make our difficulty clearer. He divides the body of the more highly developed plants into *Root* and *Shoot*. The *root* being distinguished as that part which is developed in the substratum, and also by the absence of reproductive organs, while the *shoot* is developed outside the substratum, 'produces and increases the substance of the plant' and also bears the reproductive organs. Professor Sachs developes this idea, it is needless to say, with his usual skill; the result being a highly interesting discussion on what Professor Ray Lankester has called 'homoplastic' organs, i.e. such as are not homologically related, but are forced into a certain likeness by similarity of environment. The point in which Professor Sachs's plan seems to us open to criticism is his determination to bring together, under a common name, homoplastic organs of

[1] Origin of Species, ed. i., p. 434.

radically different origins. This proceeding, to which he apparently attaches some importance, seems to us to involve the sacrifice of a useful word on the altar of uniformity. Words of everyday use are, it is true, often used in science in the manner advocated by Professor Sachs; thus we speak of the wings of insects, or the legs of a caterpillar. But many familiar words are used, morphologically, as is the case with the word 'wrist' in this sentence: 'a horse's knee is a wrist.' This is surely a convenient usage to which we may conform with advantage. Again, when we say 'an underground stem is not a root,' we use the word *root* in a morphological sense, and the meaning is clear. But if the mycelium of a mould is to be called a root, as Professor Sachs suggests, and generally speaking if we are to cease to use the names of organs morphologically, we shall soon fall into difficulties. Professor Sachs goes on (p. 6) to consider the forms which diverge from the type, under the headings, *rudimentary*[1], *reduced*, and metamorphosed or *derived* organs. This last category contains such organs as the tendril of the vine, which it is 'against common sense' to consider as degenerate. Here again we confess that Sachs's ideal physiological types do not seem well adapted for the treatment of the question. These types are in fact generalisations of the adaptations of plants to the conditions of life. The idea of the *shoot*-and-*root*-type is derived from the fact that plants are as a rule adapted both for life within and life without the substratum. The generalisation is interesting, but it seems to us more in place in the study of the environments, than in the study of the organism and its derived forms. Take such a case of metamorphosis as that presented by root-like water-leaves of *Salvinia*; surely the treatment of such a case is simpler if we adhere to the ordinary morphological point of view, than if we adopt Professor Sachs's standpoint. According to this latter view indeed, we presume that the water-leaves would be called roots if it were not for the fact that the reproductive organs are developed in them—and this seems hardly the criterion which ought to decide such a case. Fortunately however (if we may say so without disrespect) Professor Sachs does not adhere with absolute strictness to his own plan. Thus in speaking of the haustoria of *Cuscuta* he says (p. 27), 'That these latter [the

[1] *Rudimentary* is here used in the classically correct sense of a first attempt; such organs are usually known in English by the term *nascent*, while Sachs's *reduced* organs are called *rudimentary*.

haustoria] are to be regarded as reduced roots can hardly be doubtful from all the researches before us.' This can only mean that the haustoria are roots morphologically speaking. Instead of such a statement we should have expected something like the following, which we take from Professor Sachs's description of *Phycomyces*, *mutatis mutandis*. 'Our whole [*Cuscuta*] plant is devoid of chlorophyll, and is therefore unable to produce organic vegetable substance by decomposition of carbon dioxide; on the contrary it absorbs it for its development out of the substratum, that is, by means of the [haustorium] contained in the substratum which, in spite of its different organisation, behaves itself, physiologically, exactly as the root of the *Botrydium* and of the Almond, since it penetrates into the substratum urged by the same kind of irritability, and absorbs water and nutritive matters from it. *We are therefore completely justified in regarding this portion of our* [*Cuscuta*] *distinguished by botanists as the* [*haustorium*] *as its root*[1].'

If Professor Sachs had prefaced his lectures on Roots by saying, that for the sake of convenience, and in order to avoid the multiplication of technical terms, he proposed to use the word *root* for root-like organs,—no one could have objected. But, though he does not say so in set phrase, he certainly gives the impression of claiming for the organs in question the legal designation of *root*, which we could only grant them as a title of courtesy.

The fourth and fifth lectures deal with *shoots*,—typical, reduced, and metamorphosed. With the sixth lecture we find ourselves on familiar ground:—'The cellular structure of plants, protoplasm, nucleus, cell-wall.' This part corresponds in fact to the beginning of the 'Text-book,' where the morphology of the cell is the first subject treated. The facts and illustrations used are, in some measure, the same in the two books, but in the 'Lectures' we find accentuated a point of view which, as we believe, does not occur in the Text-book, and which is interesting as illustrating the later development in our author's manner of regarding nature. We allude to the secondary position in which the cell is now placed. Professor Sachs writes:—'Cell-formation is a phenomenon very general it is true, in organic life, but still only of secondary significance.' A multicellular plant is regarded as a 'cœloblast' (e. g. *Caulerpa*), in which longitudinal and

[1] The italics are our own

transverse walls have been added. Thus the plant is divided into chambers, not built up of cells.

In the treatment (p. 152) of the higher Fungi, the physiological type again comes into prominence. The author describes the closely-packed epidermal tissue, and points to the bundles 'formed of parallel elongated elements' running in the fundamental tissue, which he says are 'to be regarded as the rudiments of a vascular bundle.' Without wishing to detract from the interest of this discussion, we must point out that it is liable to misinterpretation. The student will be inclined to suppose that the vascular bundles of the higher plants are, so to speak, the lineal descendants of the strands of mycelium in the Fungus, which is far from being necessarily the case. Such points as these, and there are others of a similar kind, make us doubt whether the book is well fitted for uninstructed readers, though we give it all praise for its vividness and suggestiveness which makes it delightful reading to advanced students of Botany.

The remainder, fully three-fourths, of the volume is devoted to Physiology, and is divided into the sections 'External Conditions of Vegetable Life, and the properties of plants'—'Nutrition'—'Growth'—'Irritability'—'Reproduction.' One of the most masterly of these sections is the first, and it is a good example of the broad general treatment in which the author delights. He points out (p. 191) that all the phenomena of life arise from two factors: 'on the one hand from the structure transmitted from the mother-organism, and on the other, from external forces working on this structure.' He then goes on to show how great are the difficulties which meet the physiologist in the investigation of the first factor, since the most radical physiological distinctions give no outward and visible sign in the way of structure, but depend on differences in the 'invisible smallest particles of matter.' This leads on to the interesting discussion, in Lecture XIII, on the molecular structure of plants; while Lecture XII, dealing with the second factor (the action of the environment), treats of the general relation of plants to heat, light, electricity, etc., and completes this admirable study of the biology of plants.

It would take us too far to attempt to follow the author through even a selection of his forty-six lectures. We rejoice that under the heading 'Irritability' Professor Sachs places Geotropism and Heliotropism in the same category, an arrangement far preferable to that followed in the 'Text-Book.' This point of view was we believe first

adopted by Professor Sachs in his paper, 'Ueber orthotrope und plagiotrope Pflanzentheile,' and is now likely to become generally known and accepted.

In other points too the 'Lectures' contain expositions of the author's latest views, and in this way the translation does good service in bringing before English readers the interesting work which Professor Sachs has published in recent years. These re-statements of his results are full of interest even to those already acquainted with the original papers. But for the less instructed circle to whom the author, at least in part, addresses himself, we doubt whether this kind of mental food is nourishing, or indeed digestible. What can we expect such a reader to make of the discussion (p. 494) on the ideal construction of a dorsiventral organ out of a number of radial elements placed side by side? Or of a conception of a radial organ being formed of a dorsiventral one rolled into a cylinder?

In making these criticisms, we are far from wishing to imply that the book *as a whole* is not well adapted to the class for which it is intended. The points to which we have alluded as being likely to prove unfruitful for the less instructed, take up but a small space, and so far as our own individual taste is concerned we should regret their absence. It is as a whole that the book should be judged, and looking at it in this light we feel certain that it will do good service in guiding its readers to just conceptions of the subject.

On Hydrothrix, a new genus of Pontederiaceae.

BY

SIR J. D. HOOKER, K.C.S.I., F.R.S.

With Plate VII.

FLORES minuti, axillares, per paria spatha propria et bracteis 2 primum inclusi. *Perianthium* hyalinum, 6-lobum, lobis linearibus inaequilongis, postico latiore. *Stamen* 1, tubo perianthii insertum, lobo dorsali oppositum, filamento subulato; anthera basifixa, breviter oblonga, rimis lateralibus dehiscens; pollen minutissimum. *Ovarium* fusiforme, in stylum alabastro deflexum angustatum, 1-loculare, stigmate minuto subflabellatim 2-3-lobo; ovula plurima, placentis 3 parietalibus funiculis brevibus affixa, adscendentia, anatropa, micropyle infera. *Capsula* fusiformis, follicularis, stylo persistente terminata, polysperma, rima ventrali dehiscens, demum in valvas 3 lineares seminiferas loculicide fissa. *Semina* oblonga, teretiuscula; testa coriacea, pallide brunnea, tenuissime striata et transversim striolata; albumen sat copiosum, dense farinosum; embryo rectus, longitudine fere albuminis, bacillaris, versus extremitatem radicularem paullo dilatatus truncatus, plumula minutissima, cavitate laterali radiculae propius immersa.—Herba Brasiliensis *aquatica, immersa, caespitosa, dichotome ramosa, glaberrima, dense foliosa;* caulibus *gracilibus*, radicibus *densissime fibrosis.* Folia *fastigiatim verticillata, verticillis polyphyllis, basi vagina communi circumdatis, filiformia, flaccida, integerrima, nervis parallelis valde obscuris et canalibus resiniferis percursa; vagina infundibuliformi-campanulata, hyalina, basi folio elongato recurvo stipata, enervis.* Flores *apice pedunculi brevis v. elongati*

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sessiles; spatha propria tenuissima, hyalina, basi v. medio pedunculi inserta, folio stipata, primum ovoidea clausa, demum apice rupta truncata v. lacera; bracteae *oblongae, obtusae, hyalinae, valvatim cohaerentes, canalibus resiniferis interruptim striolatae.* Perianthium *infra medium 6-fidum, lobis linearibus obtusis, majoribus 3-nerviis, minoribus 1-nerviis.* Stylus *alabastro supra medium deflexum, stigmate antherae applicito.*

H. Gardneri, Hook. f. (Tab. vii).

HAB. BRASILIÆ TROPICÆ, prov. Ceara; in alveo arenoso fluvii Rio Sulgado dicti, inter Ico et Crato. *Gardner,* Aug. 1838 (No. 1863).

This remarkable plant has lain buried for just half a century in the many herbaria which possess Gardner's collections, and probably in all, under the category of 'Plantae dubiae affinitatis.' Though the Kew specimens had been submitted to various botanists, its relations were not recognized until the analyses which accompanied it in the Herbarium at Kew were shown to Professor Asa Gray, who suggested a comparison with the North American *Schollera graminea*[1]. Following up this suggestion for the purpose of preparing an account of the plant for the Annals, I find ample confirmation of this view; for though in all respects of habit, foliage, inflorescence and flowers, it is totally unlike any known genus of Pontederiaceae, it is unquestionably a member of that order; and a reference to the Conspectus of the Monocotyledonous families in the 'Genera Plantarum' shows that, in respect of diagnostic characters, it can belong to no other. It is evidently a flaccid annual, growing deeply rooted in the sand by its mass of capillary fibres, and by branching repeatedly from the base and upwards forming patches of considerable extent five to eight inches high. The stems are about $\frac{1}{8}$ in. in diameter, and the filiform leaves $\frac{3}{4}$ to 1 in. long by $\frac{1}{100}$–$\frac{1}{80}$ in. broad in the middle. The

[1] A. Gray, Man. Bot. North. United States, 483 (syn. *Leptanthus gramineus,* Michaux, Fl. Bor. Am. i. 25, t. 5, f. 2; Hook. Exot. Flor. t. 94). *Schollera* is now reduced to *Heteranthera,* Ruiz. et Pav. (Gen. Plant. iii. 839; Solms-Laub. in A. De Candolle, Monog. Phanérog. iv. 517).

bracts with the included flowers are about $\frac{1}{10}$ in. long, the ripe carpels, including the styles, $\frac{1}{10}$–$\frac{1}{8}$ in., and the seeds $\frac{1}{80}$–$\frac{1}{40}$ in.

Referring to the most recent monograph of the Pontederiaceae, that of Solms-Laubach in the fourth volume of Alphonse de Candolle's Monographs, it is evident that *Hydrothrix* must be regarded as either a section of the order, or as an aberrant member, characterized by foliage, inflorescence and the solitary stamen. Hitherto it has not been usual in taxonomic works to segregate individual genera as aberrant, even when monotypic, but rather to elevate them into representatives of tribes or suborders. If conceded that aberrant genera should be universally appended as such to the order of which they are regarded as members, it is impossible to lay down any rules as to the number or value of the characters that should entitle them to such local dissociation. Much must depend on the homogeneity or the contrary of the other members of the order, and something on the extent of the aberrant genus. Were *Clematis* monotypic (that is consisting of one species only), it might be better considered as an aberrant Ranunculaceous genus; but whereas it contains many species distributed over all the continents, and these form a very considerable proportion of that order, its claims are irresistible to be regarded either as a tribe, or as a separate order. The matter resolves itself into a question of convenience or expediency. Nymphaeaceae, in its larger sense, consists of six oligotypic genera, all of which are aberrant in respect of the seventh, the assumed type, *Nymphaea*. Hamamelidae[1] is another order of heterogeneous contents; it consists of about twenty genera, of which none have more than three species. But whereas in Nymphaeaceae the seven genera are all grouped under three tribes so distinct as to be considered orders by some, of Hamamelidae no genus can be considered more aberrant than another, nor can they

[1] To the fifteen genera of this order, described in the 'Genera Plantarum' in 1865, there are now to be added *Disanthus*, Maxim., *Davidia*, Baill., *Ostrearia*, Baill., and *Maingaya*, Oliv. On the other hand, *Tetrathyrium*, Benth., falls into *Loropetalum*.

be grouped under well-limited tribes. Returning to *Hydrothrix*, it differs from other Pontederiaceae quite as much or more than *Clematis* does from other Ranunculaceae, but, having regard to its habit and characters, and to its being monotypic, I prefer to regard it as an aberrant genus, rather than as constituting a tribe of the order.

Owing to the minuteness and extreme tenuity of the floral organs of this plant, and the difficulty of analysing them in herbarium-specimens, it is probable that errors in detail may be found in both the above description and in the drawing. I have, however, no reason to doubt their general accuracy. Mr. Gardner, in a note appended to the specimens sent to Sir W. Hooker, described the flowers as yellow, placed in pairs in a two-leaved membranous sheath, the perianth as 6-lobed, with the three lobes that are next the other flower more than half narrower than the other three. He further states that the plant is submerged and only flowers when the water has nearly left it. Having regard to the minute size and inconspicuous nature of the corolla in comparison with that of other Pontederiaceae, to the fact that I find pollen emitted when the flowers are still enclosed in the bracts, and that in this state the stigma is applied to the anther, it may well be that the plant is self-fertilised[1], and these flowers cleistogamous. The figures 4, 5 and 6 represent the inflorescence in this stage: it will be observed in these that the anthers appear to be opposite the ventral face of the ovary, which is, I suspect, due to distortion of the organs under compression.

Hydrothrix was elaborately studied by Mr. Benjamin Clarke, F.L.S., in 1858, who prepared analyses of it for Sir W. Hooker. Of these I have availed myself in preparing the accompanying drawing for the Annals, which is the result

[1] In Kerguelen's Land, in 1840, I found *Limosella* in flower in a lake under two feet of water and several inches of ice, with the corolla closely folded over the sexual organs, and containing a bubble of air. The anthers were full of well-developed pollen, and the ovules apparently fertilized (Flora Antarctica, vol. ii. p. 334).

of repeated dissections by myself of all the organs. Mr. Clarke describes the embryo as occasionally doubled on itself in a slight degree at the extremity most remote from the hilum, a character I have not found in the numerous seeds examined. He was at first disposed to refer the plant to Podostomaceae, but subsequently to regard it as a near ally of *Halophila*. The position of the plumule was ascertained by Mr. Clarke, and verified for me by Mr. W. Fawcett, F.L.S.

It remains to offer a few notes on the anatomy of this singular plant, which in the matter of the morphology and histology of its organs requires a more complete investigation. The stem is cylindric and terete, invested by one layer of epidermal cells with a thickish cuticle, and the epidermis is traversed by long red resin-canals. Beneath the epidermis are two or three layers of very large thin-walled cells of the cortex, which give off vertical rays enclosing air-spaces to the similar cells surrounding the central axis. The latter is very indistinctly vascular, and has a few thick-walled cells in its periphery. Very feebly developed isolated vascular bundles also occur at the outer extremities of the cellular rays. Dr. Balfour, who has kindly prepared sections showing these tissues for me, informs me that this very simple structure is what occurs in many Naiads, Hydrocharids and other water-plants, and that reservoirs of a similar red resin are found in *Eichhornia*, also a Pontederiad. The leaves, which are slightly compressed from back to front, present similar tissues to the stem, including the long resin-canals. In the delicate membrane of the spatha I find no resin-canals, but bundles of cystoliths; the latter occur also in the bracts, together with short scattered resin-canals. In the corolla still shorter resin-canals are seen. Spiral vessels are most readily detected in the bases of the leaves and in the placental tissue.

THE CAMP, SUNNINGDALE.

EXPLANATION OF FIGURES IN PLATE VII.

Illustrating Sir Joseph Hooker's paper on *Hydrothrix*.

All figures but Fig. 1 greatly enlarged.

Fig. 1. Portion of a plant of *Hydrothrix* of the natural size.

Fig. 2. Portion of a stem and branch with flowers (partly from a drawing by Mr. Clarke).

Fig. 3. Upper part of peduncle with the pair of flowers and their bracts enclosed in the spatha.

Fig. 4. Another inflorescence with the pair of flowers still enclosed in the bract, but after protrusion through the spatha.

Fig. 5. A pair of flowers enclosed in the bracts.

Fig. 6. Corolla laid open showing the leaf and stamen, with the stigma applied to the anther.

Fig. 7. Another corolla laid open and stamen.

Fig 8. More advanced flowers with the bracts open and (the corollas having disappeared) the follicles advancing to maturity.

Fig. 9. Ripe follicles and bracts.

Fig. 10. Portion of wall of ovary, placenta and ovules.

Fig. 11. Ovule.

Fig. 12. Mature follicle.

Fig. 13. The same laid open.

Figs. 14 and 15. Seeds.

Fig. 16. Longitudinal section of seed showing the albumen and embryo.

Fig. 17. Longitudinal section of embryo showing the plumule, from a drawing by Mr. Clarke.

Fig. 18. Portion of embryo with young plumule, from a drawing by Mr. Fawcett.

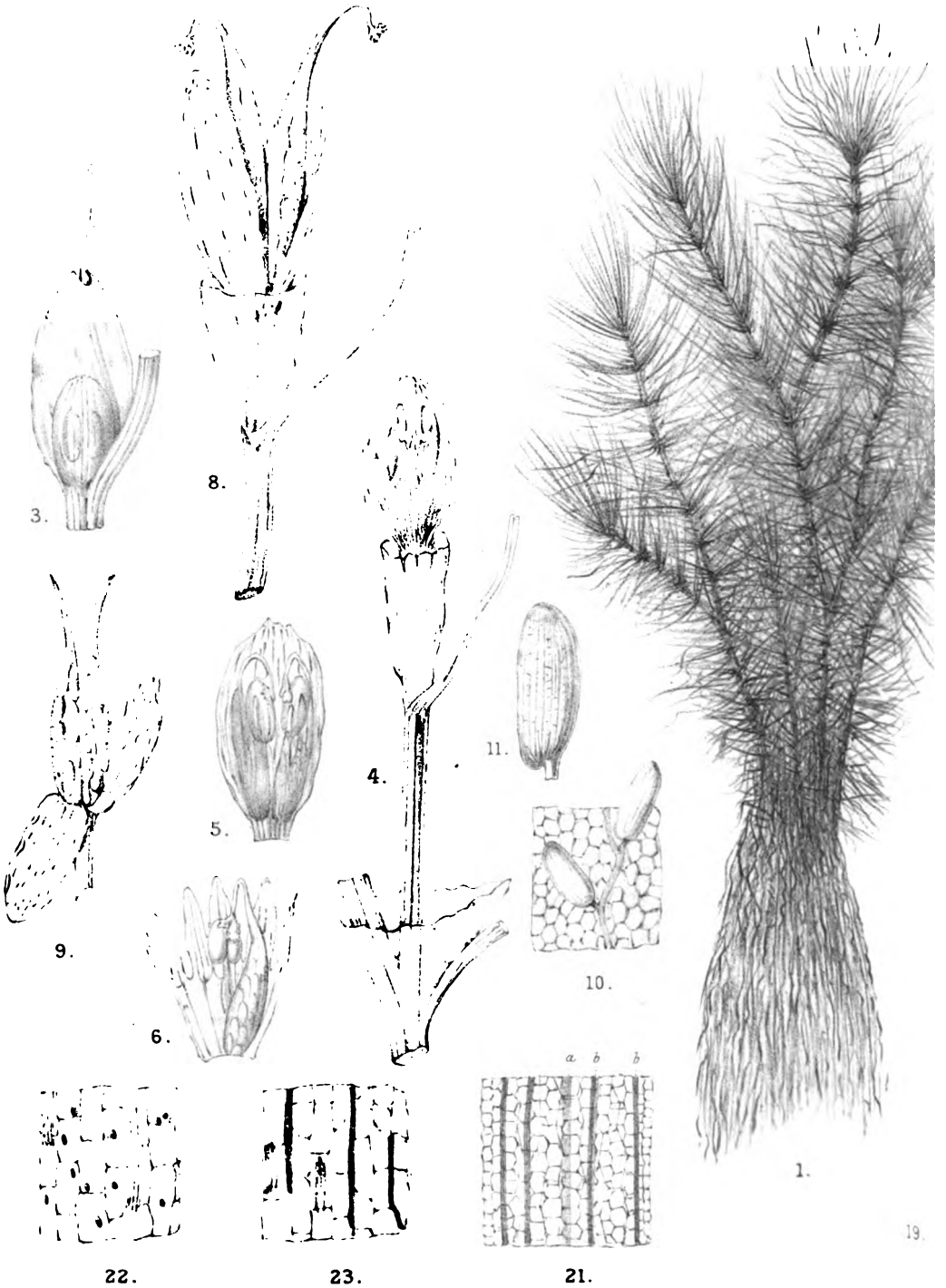
Fig. 19. Section of a portion of stem.

Fig. 20. Transverse section of portion of stem, showing, *a*, position of the peripheral vascular bundles and, *b*, resin-canals.

Fig. 21. Superficial view of portion of leaf, showing the vascular bundle *a* and the resin-canals *b*.

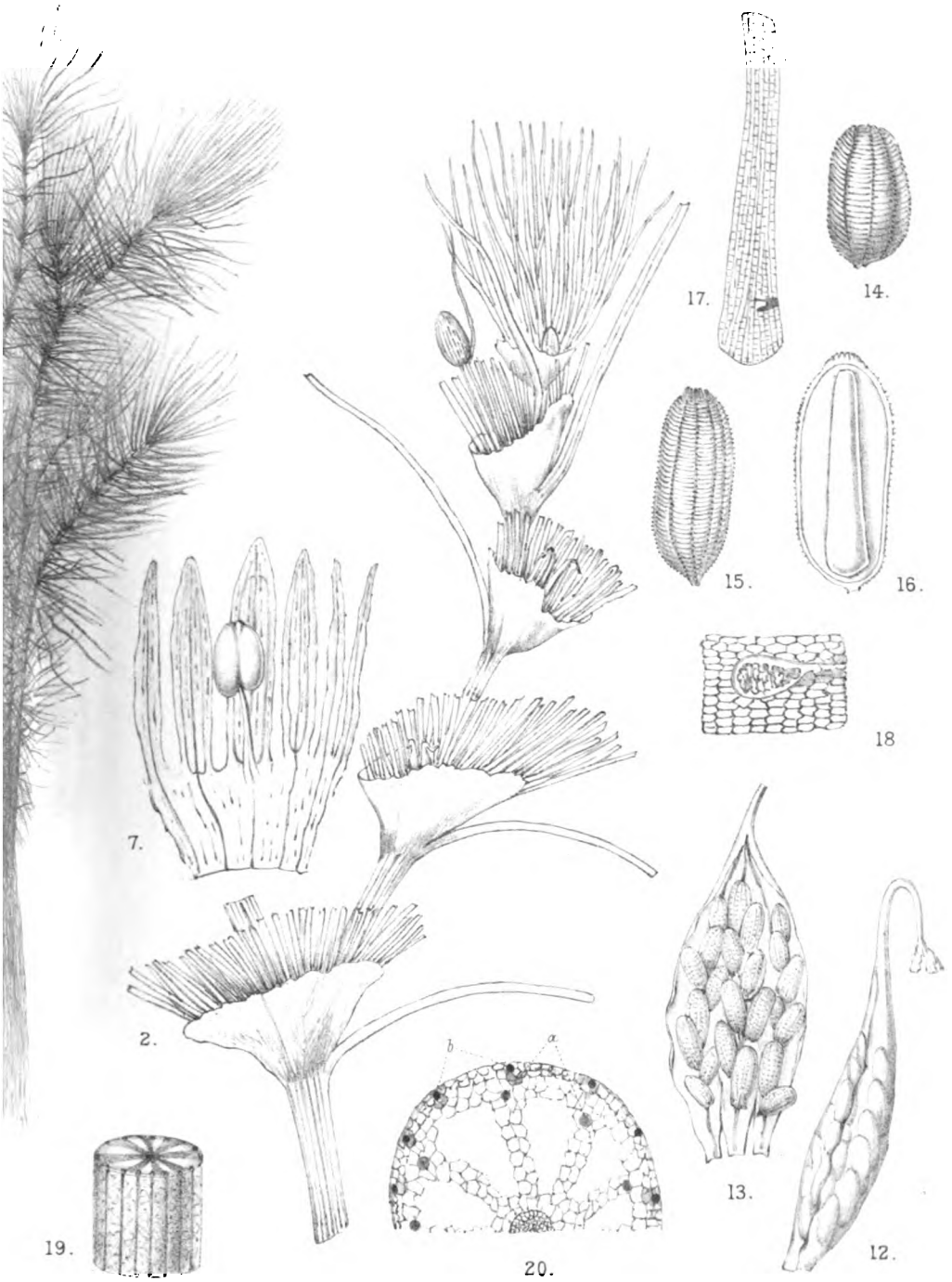
Fig. 22. Portion of tissue of the vagina showing cystoliths.

Fig. 23. Portion of tissue of bract showing resin-canals and cystoliths.



J. D. H. del

HYDROTHRIX VERTICILLARIS, Hook. f.



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On the Obliteration of the Sieve-tubes in Laminarieae.

BY

F. W. OLIVER, B.A., B.Sc., F.L.S.

With Plates VIII and IX.

THE nature of the bodies which are found in sieve-tubes blocking up the perforations has in recent years formed the basis of a great deal of discussion. These were originally discovered, it will be remembered, by Hanstein [1], and to them he gave the name of *callus*. Since their discovery our knowledge of sieve-tubes has progressed rapidly, due chiefly to the researches of Russow[2], Wilhelm[3], Janczewski[4], Strasburger[5], Fisher[6], and Gardiner[7].

Callus-plates are found universally amongst Phanerogams, but in vascular Cryptogams they are known only for a limited number of cases[8]. In the lower groups[9] of Cryptogams they are entirely unknown, indeed we have only just begun to

[1] Hanstein, Die Milchsaftgefässe. Berlin, 1864.

[2] Russow in Sitzb. d. Dorpater Nat. Ges. 1881, pp. 63–80, 1882, pp. 350–389.

[3] K. Wilhelm, Beiträge zur Kenntniss d. Siebröhrenapparates. Leipzig, 1880.

[4] Janczewski, Études comparées sur les tubes cribleux, in Mém. de la Soc. d. sc. nat. de Cherbourg, XXIII (1880), p. 300.

[5] Strasburger, Bot. Pract. I. Aufl. p. 150.

[6] A. Fischer, Ueb. d. Inhalt d. Siebröhren in d. unverletzten Pflanze, in Ber. d. deut. bot. Ges. 1885; also, Neue Beiträge z. Kenntniss d. Siebröhren, in Berl. Ges. Wiss. 1886, p. 291.

[7] W. Gardiner, Obs. on the constitution of Callus, in Proc. Cam. Phil. Soc., vol. v (1885), p. 230.

[8] i. e. *Alsophila australis*, *Balantium antarcticum*, *Osmunda regalis*, *Equisetum arvense*, according to Russow.

[9] The 'stoppers' found in connection with the perforations in many red-seaweeds require further investigation. Cf. Archer on *Ballia callitricha*, in Trans. Linn. Soc., New Series, Bot. vol. i.

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realise that such structures as sieve-tubes really occur at all so low in the plant scale.

All are agreed that amongst the higher plants the sieve-plate becomes at an early period in its history *callous*, in other words, even before the development of the perforations, a substance, possessing most characteristic chemical reactions, and known as *callus*, is found forming a thin investment of the future sieve-plate; and that after the perforations are formed, the callus being added to, becomes thickened, eventually entirely blocking up the pores and causing the *obliteration* of the sieve-tubes. The point in dispute is as to the origin of the callus, Wilhelm and Janczewski holding that it is formed by an alteration of the cellulose of the sieve-plate itself; Russow, Strasburger, Fischer and Gardiner that it arises rather from the contents of the sieve-tube.

In an investigation into the anatomy of the brown sea-weeds, more especially of the *Laminarieae*, I was struck with the very general presence in certain genera of a substance entirely resembling callus in its reactions, and in this paper I hope by an account of its mode of origin, so far as I have been able to follow it, to throw some light on this vexed question. Before entering on my own results it will be useful to briefly note what has already been done within the group of the brown sea-weeds in the same direction.

If a transverse section of any *Laminaria* (e.g. *L. digitata*) be examined a considerable differentiation of tissues will be met with. The closely-fitting and usually radially-elongated epidermal cells are succeeded by several layers of small parenchyma-cells, which, as well as the epidermal cells, are richly filled with brown pigment-bodies (phaeoplasts); within this comes a very wide zone of highly-pitted parenchyma-cells, extending almost to the centre. These are formed in a number of concentric layers, and arise by a secondary growth resembling very much the growth of the secondary wood in a dicotyledonous stem[1]. It is the central strand of

[1] Cf. Le Jolis, Examen des espèces confondues sous le nom de *Laminaria digitata*, in Nova Acta Acad. Leop. Carol. 1855.

tissue which is especially interesting to us. This consists of a meshwork of hyphae running in various directions and embedded in a mucilage formed by the breaking down of the outer layers of their walls. Amongst these hyphae a careful examination of a longitudinal section will show a number of narrow tubes running longitudinally, their walls (in alcohol-material examined in glycerin) showing a marked striation as well as stratification. These are devoid of septa except at certain points where the hypha is swollen up spherically. The septum runs horizontally across this enlarged portion, and is considered to represent a sieve-plate, as a protoplasmic continuity is demonstrable through it. These tubes have received the name of *sieve-hyphae* (Siebhyphen) or *trumpet-shaped hyphae* (Trompetenförmige Hyphen); I shall here refer to them, for brevity, always as *trumpet-hyphae*. Wille[1] was the first to carefully figure them, though Reinke[2] had previously described them; they are occasionally roughly suggested in the anatomical sketches of the older phycologists[3], who however simply refer to them as 'hyphae swollen at the joints.'

These trumpet-hyphae occur universally amongst *Laminarieae* in the medulla; I have noticed them in *Laminaria*, *Alaria*, *Agarum*, *Thallassiophyllum*, *Ecklonia*, *Lessonia*, *Macrocystis* and *Nereocystis*. Grabendörfer[4] figures them for *Lessonia ovata*. To the trumpet-hyphae I shall refer in detail later on.

No other form of sieve-tube is found in *Laminaria*, or indeed in the majority of the above quoted genera of *Laminarieae*, but in *Macrocystis* and in *Nereocystis* there is, around the central strand of hyphae, a zone of tubes with

[1] N. Wille, Siebhyphen bei den Algen, in Ber. d. deutsch. bot. Ges. 1885, p. 29; also, Bidrag til Algernes Physiologiske Anatomi, Kongl. Svenska Vetens. Akad. Handl. B. xxi. No. 12, Stockholm, 1885.

[2] J. Reinke, Beiträge zur Kenntniss d. Tange, in Pringsh. Jahrb. f. w. Bot., Bd. x. p. 317.

[3] Kützing, Phycologia Generalis, Tab. 32; Postels and Ruprecht, Illustrationes Algarum, 1840.

[4] J. Grabendörfer, Beiträge z. Kenntniss d. Tange, in Bot. Ztg. 1885.

thick walls, the width of the zone depending on the age of the part. These tubes are *true sieve-tubes*, and resemble to an extraordinary degree those of *Cucurbita*. Will[1], in an admirable paper on the anatomy of *Macrocystis luxurians*, describes these sieve-tubes carefully[2]. He did not, however, find any bodies of the nature of callus-plates, which we shall show are always developed. Nor does he, oddly enough, make any mention of the trumpet-hyphae in the central medulla. These he seems quite to have overlooked.

Nereocystis has not, so far as I am aware, been carefully investigated before, though Postels and Ruprecht[3], in their account of the sea-weeds obtained in the Lütke expedition of 1826–9, give one or two rough figures of its anatomy, showing trumpet-hyphae. In it I find the tissues to be arranged very much as in *Macrocystis*, a central medulla with trumpet-hyphae, and this surrounded by a zone of true sieve-tubes.

In *Nereocystis* as in *Macrocystis* callus is formed in the true sieve-tubes as well as in the trumpet-hyphae. In the trumpet-hyphae of other *Laminarieae* I have so far (with one exception) been unable to discover any callus. I will now proceed to describe the sieve-tubes and trumpet-hyphae of these two genera.

Nereocystis Lütkeana, Post. et Rupr.[4], is found along the North-west coast of North America, at Norfolk Sound and elsewhere. The only good general account is that by Mertens[5], who was its first scientific discoverer and named it provisionally *Fucus Lütkeanus*. When young the plant consists of a dichotomously branched 'root' with stem some

[1] H. Will, Zur Anatomie von Macrocystis luxurians, in Bot. Ztg. 1884, p. 801.

[2] I am informed by my friend Dr. D. H. Scott, that in reality Will is not to be regarded as the discoverer of these sieve-tubes. They were previously found by Professor T. J. Parker of Otago, New Zealand, but I have been unable to confirm the reference from the inaccessibility of the Journal in which they are described.

[3] Postels et Ruprechts, Illustrationes Algarum, t. 39.

[4] Postels et Ruprechts, Op. cit., p. 9. tt. 8–9.

[5] H. Mertens in Linnaea, 1829, p. 48. Translated in Hook. Bot. Misc. iii. (1833), p. 3. Cf. also Harvey, Nereis Boreali-Americana, p. 85.

30 cm. long. At its upper end the stem suddenly swells into a round bladder-nut. On this pneumatocyst are borne, as a rule, five petioles, each of which gives rise to a tuft of leaves, the leaves at this stage not exceeding 60 cm. in length. With advancing age the general aspect alters very much. the stem becomes immensely long, without any proportional increase in thickness, its diameter not being more than six to eight millimetres. The vesicle changes into a retort-shaped cylinder 2 metres long and 15 cm. in diameter, its lower end imperceptibly passing into the stem. The leaves also divide actively and attain an immense length. There may be as many as fifty leaves each 8 metres long. So far as Mertens could ascertain, *Nereocystis* is an annual. In autumn it is cast up by prevailing storms on the beach and here decays, so that next spring no traces are left.

The stem may reach a length of 80 metres, and is used as a fishing-line by the Aleutians. Nothing is known of its reproduction.

Anatomy of Stem.—Examining the transverse section of a young stem, which has as yet only reached a length of 30 cm., and a diameter not exceeding 5 mm., the tissues are differentiated into (1) a central hyphal-strand or medulla of circular or slightly oval form, its longest diameter one-fourth of that of the whole stem, (2) a broad cortex, and (3) a limiting layer or epidermis.

The medulla consists of a meshwork of hyphae, embedded in mucilage. Many of these hyphae may be seen running horizontally and taking their origin from the inmost cortical cells. Running longitudinally, and frequently branching, the 'trumpet-hyphae' are found in considerable numbers. Already at this period many of them are becoming callous. At the periphery of the medulla is the zone of true sieve-tubes making its appearance. These are arranged in radial rows about three deep, but in older stems up to six or eight. Between these sieve-tubes, which have a comparatively wide lumen as in *Macrocystis*, strands of hyphal tissue run. At present they are quite without callus. The medulla passes gradually over

into the cortical tissue, the radial rows of sieve-tubes being continued almost imperceptibly into rows of parenchyma-cells—isodiametric in transverse section—but longitudinally elongated. This parenchyma is thick-walled and strongly pitted, and its walls show very well layers of stratification when mounted in glycerin.

Towards the periphery of the stem this tissue passes over into a much thinner-walled parenchyma, with cells arranged in radial rows, and more or less radially elongated. This tissue is formed by the active division of a meristem or cambial layer arising only a few layers below the epidermis. In it are seen the young mucilage-ducts developing. They arise in a zone all round the stem at the junction of the inner thick-walled cortex and the outer cortex, which is formed from the cambial layer.

The limiting layer or epidermis consists of small and very closely-packed somewhat columnar cells. The outer wall is thick, with a well-developed cuticle. These cells, alone in the stem, contain the chromatophores with the ordinary brown colouring matter of the *Laminarieae*. The mucilage-ducts do not as yet contain mucilage; their origin is schizogenetic, and recalls forcibly that of the resin-passages from the cambium of *Hedera helix*.

In older stems, diameter about 6½ mm., a broad zone of secondary cortex has been formed, and the mucilage-ducts constitute a ring at the outer limit of the inner cortex. They have increased in size much, and their cavities are filled up with a mucilage staining brown in iodine.

In adult stems—about 8½ mm. in diameter—these ducts are seen half-way between medulla and epidermis. They branch freely in the outer cortex, never in the inner, and old ones often show an interesting development of *thyloses*, due to the ingrowth, and subsequent division in the lumen, of the secreting cells. It should be pointed out that the ducts are not everywhere lined with secreting cells, only at special circumscribed areas; often small chambers lined with secretory cells occur, these open into the ducts. The structure

and development of these ducts in this and allied genera would form the subject of an interesting account, but I do not propose to follow the subject further here.

If longitudinal sections through the medulla of an adult stem be examined after being mounted in corallin-soda, numbers of large trumpet-hyphae will be seen. These are rendered extremely conspicuous from their being full of callus which stains an intense rose-pink. The larger ones—of which one is represented in Fig. 5—attain to a diameter of ·056 mm. These occur with great frequency, and almost always have the characteristic form represented. The walls are often very thick, and the sieve-plates show fairly large perforations, though not so wide as in the true sieve-tubes. The wide part of the tube on either side of the sieve-plate is filled up with callus which can be traced a short distance along the inner layers of the wall in the narrowed portion of the tube. The shading off of the pink colour in Fig. 5 shows how far the callous change has extended.

In Fig. 9 is shown a formation of callus of somewhat exceptional character, though none the less valuable in pointing to the mode of origin of the callus. The lower portion of the figure represents the end of the callus-plug, *c.p.*, in such a trumpet-hypha as is given in Fig. 5. The callus, as is shown, has been formed by the alteration of the inner layers of the cell-wall. In one of the layers, however, the callus-formation has not been confined to the widened part of the trumpet-hypha, but a local callus-formation at *l.c.* has taken place. The layers of the wall both inside and outside this one do not in any way participate in this local change, and the inmost layer is considerably displaced owing to the increase in bulk accompanying the callus-formation. The lumen of the tube *l.* is represented black; it has been caused to deviate from its original straight course by this anomalous development. This particular case lends, I think, strong support to the view that in the trumpet-hyphae, at any rate, the *callus is formed directly from the cell-wall.* This should be compared with Fig. 10, described on page 105. Besides the type

above described smaller and often branched trumpet-hyphae are met with in fair numbers. One of these is shown in Fig. 6. The sieve-plate is on the lateral wall of the hypha, and separates the branch from the main hypha. Callus is present on both sides of the plate, quite blocking up the lumen of the main hypha, and as a glance at the figures will show, formed from the wall.

After several hours' treatment with chlorzinc-iodine the sieve-plates turn blue, the other cell-walls and the callus swell up only and do not change colour.

By cutting longitudinal sections of young stems of *Nereocystis* the trumpet-hyphae may be seen showing early stages in the development of callus. Thus Fig. 8 is taken from a stem less than 30 cm. long, and shows callus-formation before obliteration is accomplished. On the upper side of the sieve-plate callus-formation has gone much further than on the lower, and the red colouration (due to corallin-soda) extends from the middle lamella to the lumen of the hypha. On the under side only *one* layer of the cell-wall is altered, and the relation of this change to the perforations can be made out. Of three represented which pierce the inner non-callous layer only two proceed through the callous layer to the unaltered middle-lamella itself. The third one is stopped out by the callus, a fate which would soon have overtaken the others. On the upper side *all* the perforations are stopped out. I have been unable to examine younger material than this of *Nereocystis* since, as there is but one species in the genus, herbarium-material is scanty, and a certain reserve must be exercised in damaging unique specimens.

Regarding the *true* sieve-tubes themselves, little need be said, since they do not essentially differ from those in *Macrocystis* of which I have had a much greater amount of material at my disposal. They arise at the periphery of the medulla, and are much branched. Fig. 20 gives an idea of their structure before the development of the callus. Running down the centre of the tube and spreading over the sieve-

plates is the contracted protoplasmic content of the tube. Gradually as they get older callus is formed, and the pores obliterated. My description of the same structures in *Macrocystis* must however suffice.

Macrocystis pyrifera, Ag.—The best general account of this plant is given by Hooker and Harvey[1]. According to these authors all the different species are in reality varieties only of *M. pyrifera*. Many so-called species may be found growing on the same plant. It is an inhabitant of antarctic seas between lats. 40° and 64° S. It is found extending along the Pacific coast of America as far north as California and the Aleutian Islands; on the Atlantic side, not beyond the Plate River, lat. 35° S. Its immensely long stems, reaching to 200 metres, and leaves with bladders, are too well known to require further description here. Regarding its fructification, all that is known is that within a few centimetres of the root, submerged leaves[2], destitute of floats, are formed with sori, consisting of patches of 'spores.'

Anatomy of Stem.—In the general anatomy there is no essential point in which it differs from *Nereocystis*. The outline of the central medulla is usually oval rather than round. In almost all cases the zone of true sieve-tubes completely encloses the axile hyphal strand; this I found a constant character in 26 out of 28 specimens examined. The only exceptions were *Macrocystis planicaulis*, in which at one side of the medulla the hyphal tissue ran into the cortex, the zone of sieve-tubes being discontinuous at this spot; and in a specimen of *Macrocystis angustifolia*, in which a most interesting arrangement was met with. The transverse section was crescentic, the dorsal side concave, the ventral convex. The medulla, oval in outline, was situated so that its longest axis coincided with the plane of symmetry (median plane). On all sides except the uppermost it was enclosed in a zone of sieve-tubes, but at this point the inner hyphae came into

[1] Hooker's Flora Antarctica, vol. ii. p. 461.

[2] Cf. Gardiner, On the occurrence of reproductive organs on the root of *Laminaria bulbosa*, in Proc. Camb. Phil. Soc. vol. v (1885), p. 224.

very close relation with a narrow groove which ran longitudinally along the middle of the dorsal surface. At some places a split seemed to extend quite down to the medullary hyphae. What this arrangement may signify I know not, unless it be to enable a certain amount of the mucilage formed between the hyphae to be discharged to the exterior. No mucilage-ducts were developed on the concave dorsal surface, but plentifully enough around the convex and right up to the tips of the horns of the crescent. With these two exceptions the zone of sieve-tubes was continuous, the sieve-tubes themselves being arranged in radial rows, each row in old stems being made up of as many as 10 or 12 tubes. In almost every species of *Macrocystis* the 'bundle' is enclosed in a well-developed collenchymatous sheath, some 8 or 10 layers broad, passing over externally into the ordinary cortical parenchyma.

In the medulla run frequent trumpet-hyphae, formed on the same type as in *Nereocystis*, but, generally speaking, more often branched. In all but the youngest stems these trumpet-hyphae are callous—the callus being formed apparently from an alteration of the *wall*. Fig. 1 is a simple hypha with callous plate from *Macrocystis luxurians* drawn as seen in corallin-soda. In Fig. 2 a large trumpet-hypha from *Macrocystis pyrifera* is shown; here it can be seen clearly enough that it is the *wall* which gives rise to the callus; Figs. 3 and 4 from *M. pyrifera* show an excessively common mode of branching of these hyphae—similar to that met with in *Nereocystis* (Fig. 6). Variations of this type occur; as for instance that given in Fig. 11 (from the medulla of *M. planicaulis*), where the main trunk of the hypha divides just in front of a sieve-plate. The callus-formation is shown exceedingly well in this diagram. Sometimes a branching of the most complicated nature occurs; such a branched system of trumpet-hyphae is indicated in Fig. 13 from a specimen of *M. pyrifera* brought from the Cape of Good Hope by Brand in 1790. All the sieve-plates in this are callous; the walls of the hyphae connecting them are not completely involved in

the callous degeneration, as may be seen from the shading off of the red in the figure.

Regarding the development of the callus in the trumpet-hyphae; this begins quite early in their history, and may be seen commencing in Fig. 7 in *M. zosteraefolia*. At this time the walls are much swollen up as compared with still younger stages. The layer of the wall which first alters, i.e. that coloured pink in Fig. 7, is the outermost one next the middle lamella. At first this change occurs only opposite the sieve-plate, then later extending a certain distance down the sides of the trumpet-hypha. Later still the *inner* layers become similarly altered. In this figure I have not represented the perforations as shown in Fig. 8 [*Nereocystis Lütkeana*]. They are very fine, appearing as mere striae. As I have already said, the narrow parts of the trumpet-hyphae are sometimes involved in the callus-formation. Usually this change passes along them centrifugally from the sieve-plate. In one specimen of *M. luxurians* examined I found that the callus change commenced at many points in the narrower parts of the hyphae, quite independently—though simultaneously—with the change in the dilated portion. This is seen in Fig. 10, and is most important when considered in connection with Figs. 7, 8 and 9.

At the regions other than those marked A and A^1 the wall has completely broken down into callus; and by the swelling up involved in this change the lumen is obliterated; *o. l.* represents this lumen dwindled to a mere line. At A callus formation has not yet commenced and the hypha is here in its normal condition, and a distinct lumen is present. At A^1 callus-formation has progressed, but the inmost layer is not yet entirely converted here. When the whole hypha has undergone the alteration it will be no longer constricted, and will show no traces of the intermittent manner of the change.

Leaving now the trumpet-hyphae, I will go on to describe the appearances met with in the *true* sieve-tubes. These tubes are fairly wide, running longitudinally in the zone around the central hyphal strand. Their average width is about ·061 mm.

in the various species of *Macrocystis*, the sieve-plates being for the most part horizontally placed, dividing up the sieve-tube into members. As a rule sieve-plates will occur every ·2–·25 mm. in any tube. These plates are perforated by large circular or, more usually, polygonal pores. The plates indeed forcibly recall those in *Cucurbita*. Sieve-plates are also found in great numbers on the longitudinal walls, occurring wherever two tubes run adjacently. These plates may be either on the radial or on the tangential walls. Fig. 14 is a longitudinal radial section through two sieve-tubes of *M. pyrifera*. Where they impinge on one another they are separated by a vertical sieve-plate. In the figure are seen sieve-plates (on which are developed thick callus-plates, coloured red) in all three planes. The protoplasmic content, *p*, lies contracted in the centre of the tube, spreading out however over the sieve-plates and forming the familiar *Schlauchköpfe* of German authors.

It is to be noted that the horizontal sieve-plates are always larger than those on the vertical walls, and also that the perforations of the former are wider than those of the latter. This is not surprising, for, assuming these sieve-tubes to function here as they do in higher plants, it is obvious that the requirements for transport of plastic material in such a plant as *Macrocystis* must be very much greater in a longitudinal than in other directions; hence the larger horizontal sieve-plates with large perforations. These perforations have an average width of ·003 mm. On the older sieve-plates, both horizontal and vertical, a well-developed callus-formation is found. This ultimately becomes very thick and completely obliterates the perforations. The thickness of the whole callus-development of both sides of any sieve-plate may reach as much as ·075 mm., though in most specimens such a great thickness is not attained. In these sieve-tubes, as opposed to the trumpet-hyphae, there is no callus-formation in connection with the wall other than at a sieve-plate. This callus, as I shall show later on in this paper, gives reactions identical with the ordinary phanerogamic callus, and must be regarded as the same substance. The fully-developed callus-plates normally

are quite structureless when examined unstained, or in corallin-soda, Hoffmann's blue, or Russow's reagent. With hydric sulphate, as they swell up, a well-defined stratification may be made out, the lines of stratification being parallel to the free surface of the callus-plate. A similar appearance may be made out in chlorzinc-iodine. Fully formed callus-plates are shown in Figs. 15, 16, and 17. Figs. 15 and 16 are from *M. pyrifera*, collected ninety years ago. In Fig. 15 depressions are seen which are continued some distance through the callus-plate towards the sieve-plate. This, however, none of them reach. These lines are all that represent the original perforations of the sieve-plate which have become obliterated by the callus. In Fig. 16 less trace even than this is seen of the perforations. As a rule, however, the ends of the callus-plates have a number of conical depressions, as in Fig. 17 [*M. planicaulis*]. Into these continuations of the contracted contents of the tube are produced—ending of course blindly. In some cases in which the contents (*Schlauchköpfe*) have been pulled away from the callus-plate, in making the preparation, it can be seen that on its surface (previously in contact with the callus) are a number of elevations, which correspond to the depressions in the callus. Out of more than two dozen specimens of Macrocystis collected at various periods I have not met with a single instance in which callus-plates are absent from the older true sieve-tubes.

Before entering on the development of the callus-plate I will speak briefly of the contents of the sieve-tubes. In studying this, herbarium-material is of little value. As a rule the contents are seen as a retracted sac with ends widened over the sieve-plates (*Schlauchköpfe*). This sac is granular and stains light brown in iodine. Sometimes I have found what seemed to be drops of mucilage in it, attached at various points to its outer layer, or even as small aggregations in the region of the sieve- or callus-plate.

In only two cases have I found the contents not contracted but consisting of apparently a coagulated mucilage enclosed in a thin membrane—the 'primordial utricle.' This mucilage

stains a rich golden-brown in corallin-soda, and in both cases in which I have found it well-developed callus-plates have been present. One of the specimens showing it [taken in 1779] had a small wound which cut through the zone of sieve-tubes *on one side* only. No doubt this cut was inflicted during the life of the plant, for the sieve-tubes cut into all showed this curious condition for some millimetres on either side of the cut. The undamaged tubes were quite normal. This condition is no doubt a pathological or protective arrangement. Any further account of the contents and changes of these sieve-tubes must be reserved until I have an opportunity of examining fresh or properly preserved material.

Callus commences to develop early in the history of the sieve-tubes. At the time of perforation, so far as I can ascertain, the sieve-plates are not callous, hence differing from the cases of *Vitis*, &c., in which the plate is slightly callous even before perforation [1]. Soon enough the sieve-plate becomes invested in a complete covering of callus, not only on the upper and lower surfaces of the cellulose-framework, but also lining the pores. The sieve-plates would appear to be in this condition during the greater part of their functional activity, becoming obliterated from a further later development of the callus. If a fairly old stem be examined, in which the zone of sieve-tubes is about eight sieve-tubes broad, all the older and inner ones will be found to be completely callous; this will apply probably to the inner five rings. The sixth and seventh will as a rule be slightly callous, but not yet obliterated, and the outmost tubes of all will show no callus-formation of any kind. This arrangement is a fairly constant one. In very young stems only the inmost will show any trace of callus. The trumpet-hyphae, however, become obliterated much earlier, i. e. by the time that two or three rings of true sieve-tubes are formed. In Fig. 19 an early stage in the development of the callus (from *M. Orbignyana*) is shown. The callus (stained red) is formed all round the cellulose-frame-

[1] Cf. Wilhelm, loc. cit.

work by—I am inclined to think—an alteration of the wall itself. In the figure the pores, though considerably narrowed, are not as yet obliterated. For the sake of clearness I have omitted to represent the protoplasm, continuous from one member to another through the pores. Fig. 18 is an interesting case of unequal thickening of the callus-plate on one side (from *M. Orbignyana*); such are quite rare.

I have never found any connection between the trumpet-hyphae and true sieve-tubes either in *Macrocystis* or in *Nereocystis*, though they run often very close together.

Before concluding this paper it will be well to describe in detail the micro-chemical reactions given by the callus. We can then see how we are justified in considering it identical with the callus of phanerogamic sieve-tubes.

Nature of the Callus.—It has been already stated that the micro-chemical reactions shown by the callus occurring both in the trumpet-hyphae and in the sieve-tubes proper of *Macrocystis* and *Nereocystis* agree almost absolutely with those characterising the callus of the phanerogamic sieve-tube. These it will be remembered are such that callus cannot be confused with any ordinary mucilage. The following are the results given by the callus in the two genera:—

(1) *Russow's callus-reagent.*—This consists of a mixture of equal parts of chlorzinc-iodine and iodine in potassic iodide; it was used with great success by Russow and by Wilhelm, and is considered to be the most delicate callus-test. With it callus is stained a deep brown. This was the case with the callus of *Macrocystis* and *Nereocystis*. The unaltered cell-walls stain yellow. When mounted in this reagent the partially obliterated perforations show up very well, and in early stages of callus-development the thin layer of callus could be easily distinguished from the cellulose sieve-plate.

(2) *Corallin-soda.*—This reagent is due to Szyszylowicz[1].

[1] Szyszylowicz, Osobne. vobicie z. Rospan Akad. Umicj. w. Krakowiz, x. 1881.

It is prepared by adding rosolic acid to a strong aqueous solution of sodium carbonate. The dye so obtained stains the callus with great avidity a brilliant rose-pink. Unfortunately the stain is not a permanent one, as preparations mounted in glycerin gradually fade, and in about four days' time are almost colourless. It is further necessary to use this reagent freshly made up. For forty-eight hours after making it will stain well enough, but after this period this capacity is gradually lost. With the callus-plates in question I obtained most satisfactory results; they stained indeed as satisfactorily as those of *Cucurbita* could.

(3) *Bismarck-brown* dissolved in water is also a reagent which stains callus. It is not so satisfactory as the above, or as Hoffmann's blue, since the whole section is stained by it, though it should be pointed out that the different layers of the cell-wall are very beautifully differentiated. In the callus-plates of the sieve-tubes proper of *Macrocystis* I was able, with this reagent, to make out a very decided stratification. This reagent acts best when recently made up.

(4) *Hoffmann's blue.*—This is probably the soluble aniline blue used by Russow[1], and considered by him to be an eminently characteristic callus-reagent. I always used it dissolved in 50% of alcohol, and obtained the best results with the callus-plates in question. Sections should remain in it twenty-four hours, and be then washed in water and mounted in glycerin. Under these conditions the colour is not retained in the cell-walls, but the callus-plates remain a very brilliant blue, which is permanent. I have preparations which have been made for three months, and exposed to the light all the time, and so far have not at all faded.

(5) *Chlorzinc-iodine* does not, as a rule, stain the callus-plates in *Macrocystis* or *Nereocystis*; they swell up under its action and show stratification. In a young specimen of *Nereocystis Lütkeana* is a trumpet-hypha about the same

[1] Russow, Callusplatten bei den Gefässpflanzen, in Sitzb. d. Dorpat. Nat. Ges. 1881, p. 63.

stage as that represented in Fig. 7, the layer of callus next to the sieve-plate, and which is coloured red in this figure, stained violet. I imagine this layer was not as yet completely converted into callus; in other cases the *inmost* layer was coloured violet, and not the one next the sieve-plate. In all cases the sieve-plate itself turned blue.

(6) *Methylene blue.*—With this reagent negative results were found. The callus was not stained by it, nor by the majority of other aniline dyes. Eosin (in water) coloured the callus-plates a faint red, but only lasting so long as the preparations were kept in the stain. These negative results with Methylene-blue are highly characteristic of all callus.

(7) *Haematoxylin.*—With dilute solutions the callus-plates stain deeply.

(8) *Hydric sulphate.*—As this is run in, the callus-plates gradually swell up, showing at the same time a very beautiful stratification. The swelling up goes on and the callus gradually becomes indistinct, and is finally dissolved. By dissolving away the callus in cases where the pores are not yet obliterated the connecting threads may be demonstrated by staining in Hoffmann's blue, which shows them up in a very effective manner.

(9) *Potash.*—Here also the callus swells up and becomes later indistinct; I did not see however that it absolutely dissolved as in the case of the hydric sulphate.

It will be seen from this series of reactions in which the Laminaria-callus agrees with that found in phanerogamic sieve-tubes that the two substances are to be regarded as identical. This is the more remarkable from the fact that in hardly any other plants but Phanerogams is any callus found.

In addition to the above enumerated reactions it should be mentioned that I find the Laminaria-callus to be *isotropic*. In this it further agrees with phanerogamic callus.

The capacity for its development in these two sea-weeds is no doubt connected with the fact that both *Macrocystis* and *Nereocystis* attain to such a gigantic length without any

corresponding great increase in the diameter of the stem. No other sea-weed approaches them in this respect, and it is significant to note that in none other than these two are true sieve-tubes—in addition to mere trumpet-hyphae—known to exist.

I must reserve a full discussion of the question of the origin of callus in sieve-tubes generally until such time as I may have had opportunity of examining its development in *Macrocystis* etc. in fresh material. Here I can only repeat that I am strongly of opinion that, in the case of the trumpet-hyphae, it is formed by an alteration of the cell-wall itself. This view will be fortified by an examination of the figures attached to this paper—especially Figs. 7, 8, 9 and 10. In the true sieve-tubes it is at present impossible to give a decision, though one might infer that, since in the trumpet-hyphae it is formed from the *wall*, it has a similar origin in the sieve-tubes proper. All I can safely say is that, so far as I have gone, my results on the origin of callus in *Laminarieae* tend to confirm the opinion of Wilhelm and Janczewski, referred to on page 96, rather than the opposing view of Russow, Fischer, and Gardiner.

It is not, I think, without some instructiveness to draw a certain comparison between these two sea-weeds—*Macrocystis* and *Nereocystis*—and climbing or twining Phanerogams. Like the climbers, both differ from their allies in that the stems have an extremely small diameter when considered in relation to the length of the whole plant. In neither does the stem develope mechanical tissues necessary to support it. The case is very different in, say, *Lessonia*—an allied Laminaria—which stands erect like a submerged tree, with stem almost as thick as a man, with long-continued secondary growth in thickness. Just as the climber is supported by its special organs of climbing, so are these two supported by their floats. In *Macrocystis* it is the leaf-petioles which are modified in this way, in *Nereocystis* the whole upper portion of the stem is dilated and forms one gigantic pneumatocyst.

In climbers there is, as a rule, a tremendous development of

sieve-tubes[1]. It is only necessary to quote the beautifully developed sieve-tubes in *Cucurbita*, *Lagenaria*, *Vitis*, *Humulus*, *Tamus communis*, etc., which are conspicuously wider, and have wider perforations than in the generality of other Phanerogams. So in *Macrocystis* and *Nereocystis*. In these alone of all the *Laminarieae* we find true sieve-tubes, and these with very large plates with wide pores; and in addition to this, the perfection of the mechanism by a callus-development. The causes necessitating the presence of such highly developed organs for the transport of plastic substances are, there can be little doubt, in both cases much the same.

In conclusion, I think it must be fairly obvious that in these two plants we have to deal with what may be considered a well-differentiated vascular bundle—at least so far as the phloem is concerned. That this bundle is in any way homologous with that of higher plants is a matter beyond the province of this paper to discuss. Indeed, I believe rather the line of descent of higher plants to have diverged long since from the stock from which the *Laminarieae* arose.

To me one of the more interesting results of this investigation is to confirm the opinion of systematists as to the close affinity existing between the genera *Macrocystis* and *Nereocystis*, although there is a considerable diversity of external form. In the great treatises on Algae[2] they are united closely together, although the determination was not based on their internal structure, of which little was known at the time; nor on their reproduction, concerning which nothing is known in *Nereocystis*, and in *Macrocystis* the presence of 'spores' on late-arising adventitious shoots or leaves in the neighbourhood of the root is all that has been ascertained[3]. It remains then a most interesting point to solve the mode of reproduction in these two genera, and to see how far their agreement bears out their near affinity as based on the minute structure of their

[1] G. Haberlandt, Physiologische Pflanzenanatomie, p. 222.

[2] Kützing, Species Algarum, p. 584.

[3] Cf. W. Gardiner, On the occurrence of reproductive organs on the root of *Laminaria bulbosa*, in Proc. Camb. Phil. Soc. Vol. v (1885), p. 224.

vegetative organs. The placing of these genera together I can but ascribe to that wonderful 'instinct for affinities' possessed by great systematic botanists. As investigation into minute plant-anatomy is pushed further and further, this characteristic of correctly gauging the true systematic position of a plant from external data only is repeatedly seen; thus, to give another instance, Scott[1], in his investigations into the distribution of laticiferous tissue in *Euphorbiaceae*, finds himself able to confirm on purely histological grounds Bentham's separation of certain tribes on ordinary macroscopic data.

This investigation has been conducted entirely on dried herbarium-material, but I have always been able to confirm my results by the examination of a great number of specimens which have been collected at various epochs by Bond, Banks, Hooker, Harvey, Lyell, Moseley, and others. I have material taken as long ago as 1774 up to as recent a date as 1874 by the 'Challenger' expedition. I wish to take this opportunity of thanking Mr. J. R. Jackson of the Kew Museums, and Dr. Carruthers and Mr. E. G. Baker of the Natural History Museum, all of whom have very liberally put material at my disposal.

My mode of procedure has always been as follows:—The dry pieces were placed in water for several hours—sometimes even twelve—during which time they absorbed very much, and swelled up often to four times their original diameter when put in. They were then placed in weak spirit, and after a few hours' stay in this they were in very good state for preparing sections. The material was now transferred to stronger spirit and kept in this way any length of time.

I am fully aware that it may be urged as an objection against my results that these callus-plates are simply aggregations of a peculiar mucilage artifically induced by my method of softening dry herbarium-material, seeing that I have not, as yet, confirmed them with fresh material. To this I need only

[1] D. H. Scott, Articulated Laticiferous Vessels in *Hevea*, in Linnean Soc. Journal, Bot. Vol. xxi. p. 572.

point out that their distribution, relation to the sieve-plates, and various stages of development in tubes of varying age (bearing, as they do, such a striking similarity to what occurs amongst Phanerogams) entirely precludes their being due to any such chance cause. They are no doubt as natural and essential a part of the sieve-tube mechanism of the plants in question as amongst the higher groups.

Summary of Results.

I. All members of the *Laminarieae* possess an axile strand, in which are found numerous *trumpet-hyphae*.

II. In two genera only, *Macrocystis* and *Nereocystis*, are true sieve-tubes found in addition to trumpet-hyphae.

III. In these two genera the trumpet-hyphae and the true sieve-tubes become in time obliterated by the development of callus on the sieve-plates in a manner comparable to the obliteration in the sieve-tubes of e. g. *Cucurbita*.

IV. This callus is identical in all its micro-chemical reactions with the callus of phanerogamic sieve-tubes, and may be regarded as chemically the same substance.

V. The callus is formed by an alteration of the *cell-wall* in the trumpet-hyphae.

VI. As a result of the investigation, *Macrocystis* and *Nereocystis* have been rightly very closely associated by systematists.

Jodrell Laboratory, Kew.

EXPLANATION OF FIGURES IN PLATES VIII AND IX.

Illustrating Mr. F. W. Oliver's paper on the Obliteration of the Sieve-tubes in Laminarieae.

[N.B.—The figures are coloured in red to show the callus as stained with corallin-soda.]

Fig. 1. *Macrocystis luxurians.* A typical trumpet-hypha showing well-developed callus-plate. (× 750.)

Fig. 2. *Macrocystis pyrifera.* Large trumpet-hypha showing very well the mode of origin of the callus by an alteration of the cell-wall. (× 750.)

Figs. 3, 4. *Macrocystis pyrifera.* Showing modes of branching of the trumpet-hyphae. In 4 the development of callus has proceeded some distance along the left-hand member. (× 750.)

Fig. 5. *Nereocystis Lütkeana.* Dilated portion of trumpet-hypha from an adult stem, showing very massive callus-development. (× 700.)

Fig. 6. *Nereocystis Lütkeana.* Showing a common form of branching met with amongst the trumpet-hyphae. (× 750.)

Fig. 7. *Macrocystis zosteraefolia.* Trumpet-hypha from a young stem showing the commencement of callus-formation. It will be noticed that the inmost layer of the wall is not coloured and as yet is not affected by the callus-transformation. The layer outside it—coloured a faint pink—is being altered into callus. (× 500.)

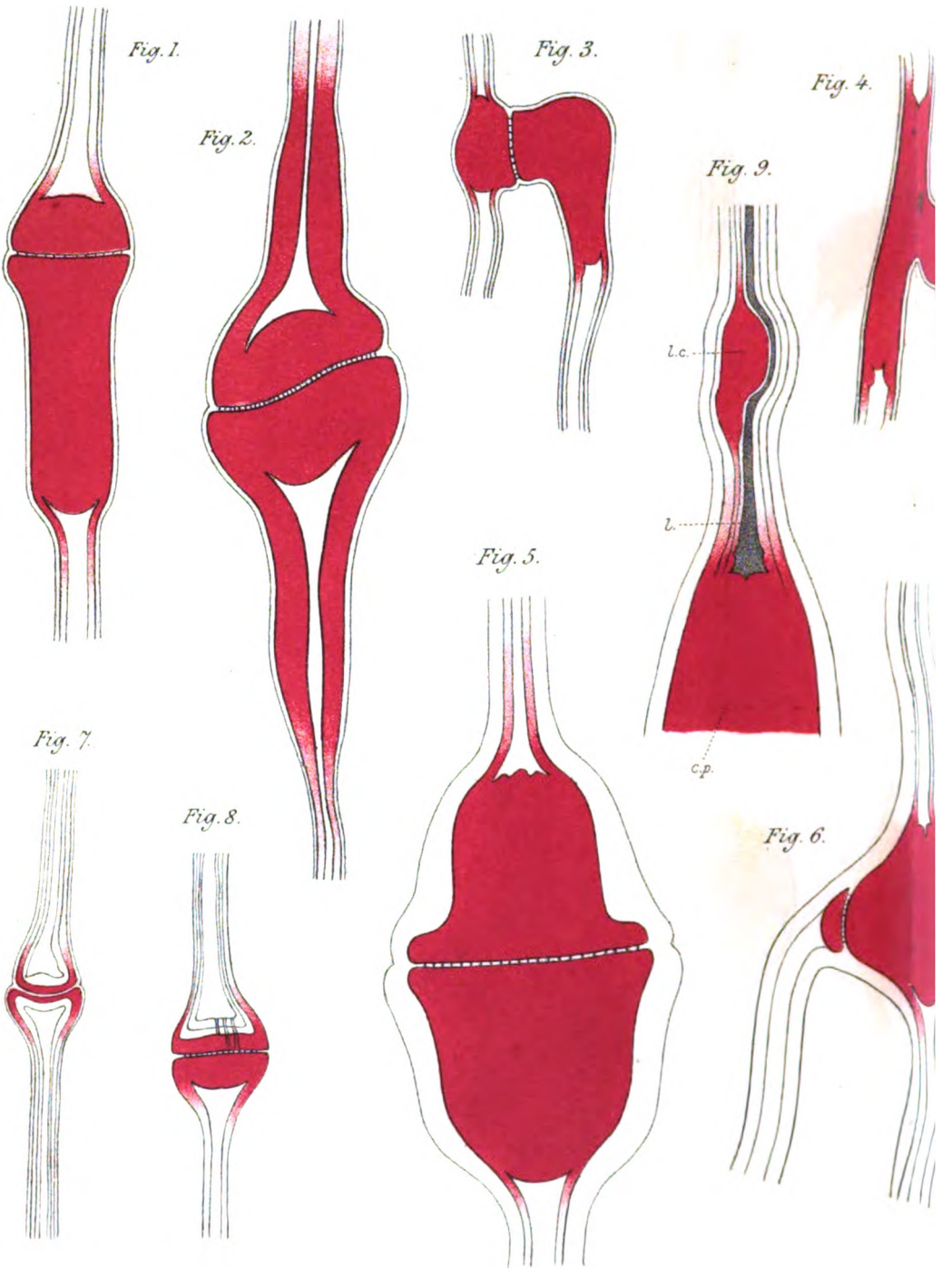
Fig. 8. *Nereocystis Lütkeana.* This preparation is somewhat similar to that figured in 7. Several perforations are shown, as yet not quite blocked by the callus. One of these only reaches as far as the callus-layer, the other two quite to the middle lamella. (× 500.)

Fig. 9. *Nereocystis Lütkeana.* Preparation showing a local callus-formation some distance from the sieve-plate of the trumpet-hypha. The local callus-formation, *l. c.*, is seen to be in the inmost but one stratum of the wall of the tube: the inmost layer may be seen bending round it. The lumen, *l.*, of the tube is represented black. Owing to the callus-formation at *l. c.* it deviates considerably from its course. At *c. p.* is represented the ordinary callus-thickening of the trumpet-hypha. The sieve-plate is not represented. (× 700.)

Fig. 10. *Macrocystis luxurians.* Showing a piece of a trumpet-hypha a considerable distance from any sieve-plate, in which the callus-formation is extending the whole length of the tube. At parts other than *A* and A^1 the whole wall has broken down into callus and the lumen is obliterated by the swelling up involved in this change. *O. l.* represents the remains of the lumen; at *A* callus-formation on the wall has not yet taken place, and at A^1 the inner layers are not yet completely converted. (× 800.)

Fig. 11. *Macrocystis planicaulis.* Trumpet-hypha branching in close proximity to a sieve-plate. Callus-plates extremely well developed. (× 750.)

Fig. 12. Wide trumpet-hypha from an unnamed *Laminaria* from Vancouver's Island with callus-plates. (× 750.)



F. W. O. del.

OLIVER.— OBLITERATION OF SIEVE-TUBES IN LAMINARIEÆ.

Fig. 10.

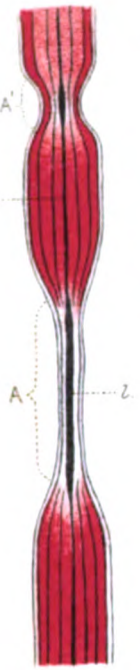


Fig. 12.

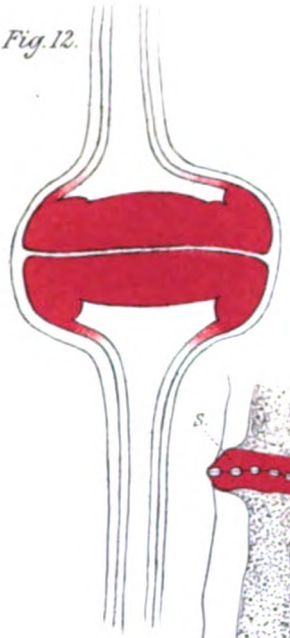


Fig. 13.

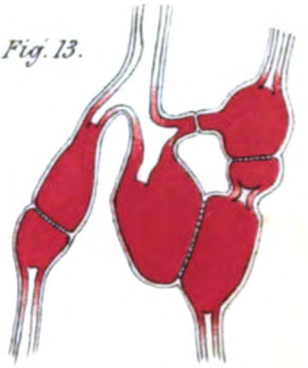
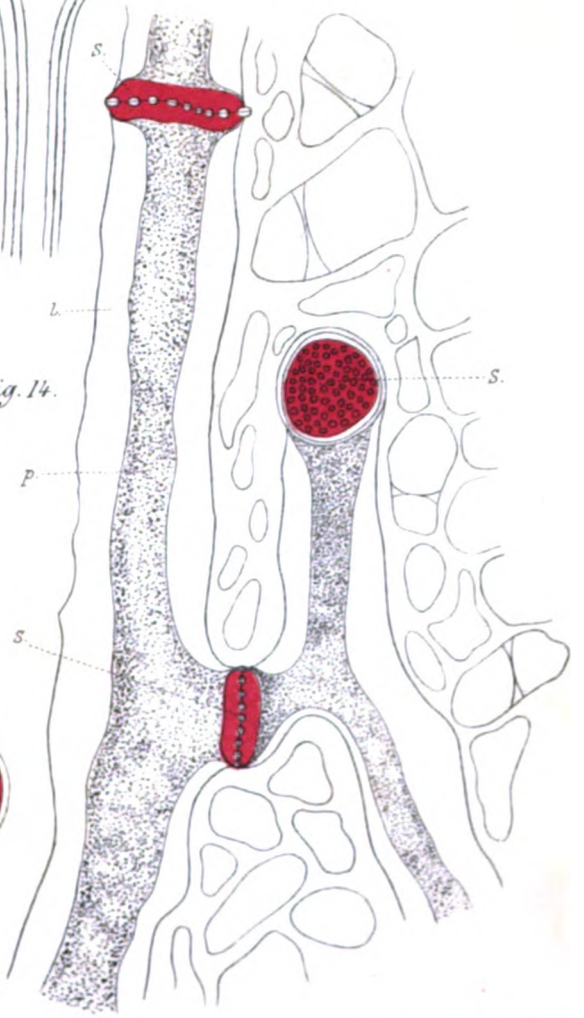


Fig. 11.

Fig. 14.



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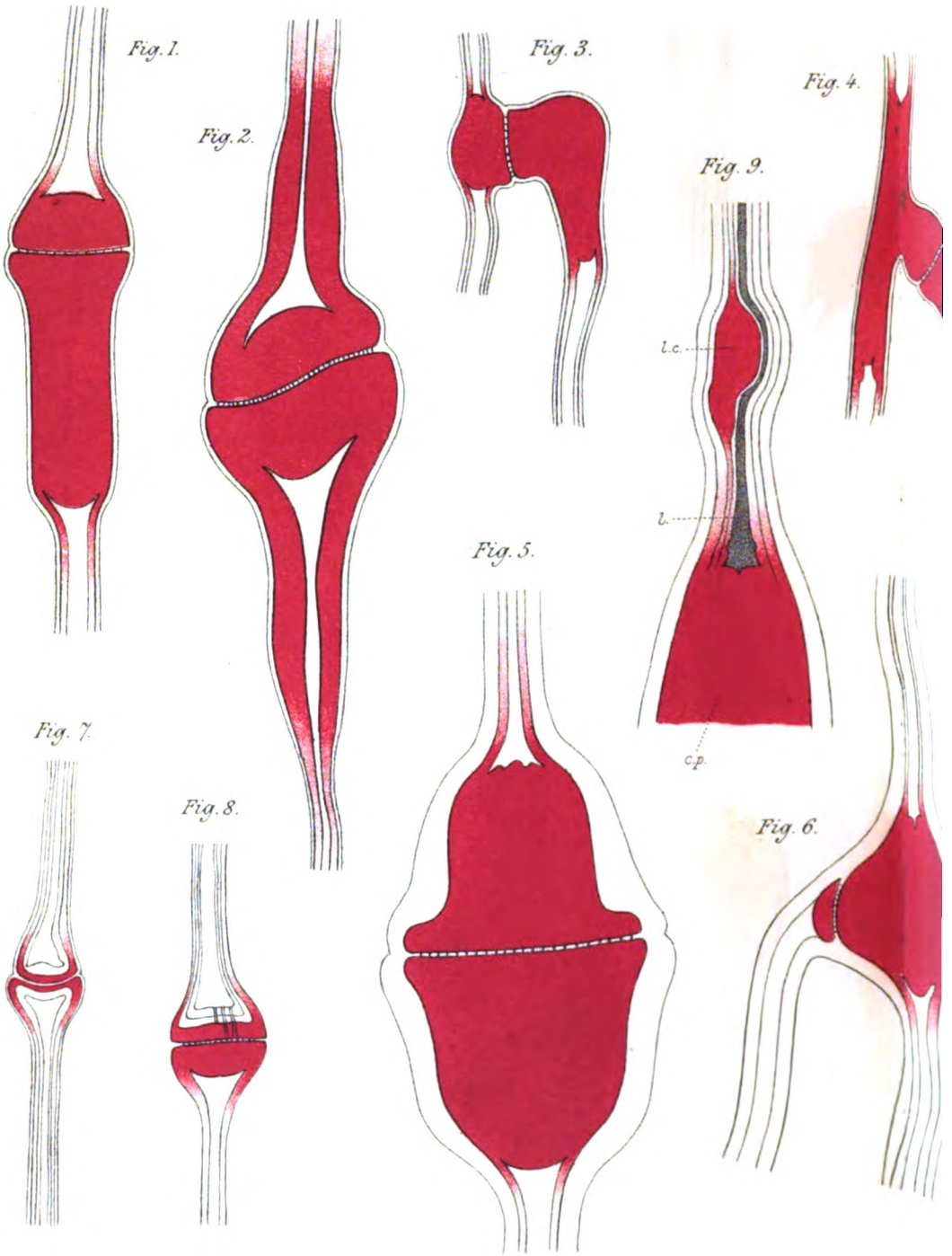

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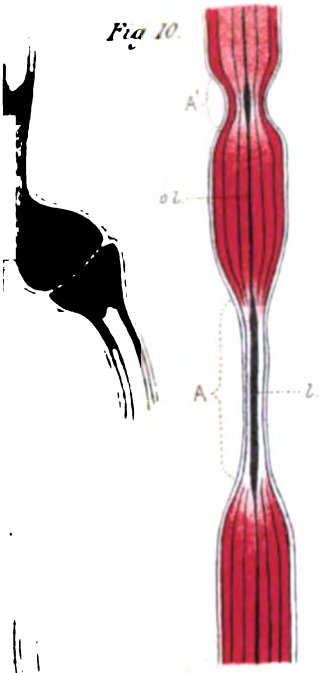
OLIVER.— OBLITERATION OF SIEVE-TUBES IN LAMINARIEÆ.

Fig 10.



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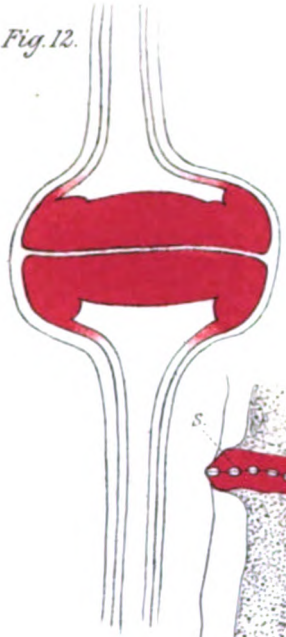

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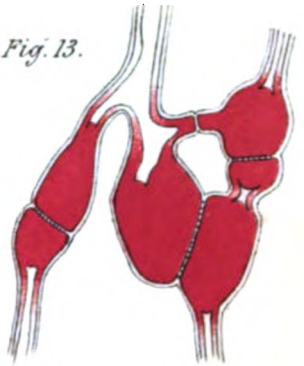

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Fig. 14.

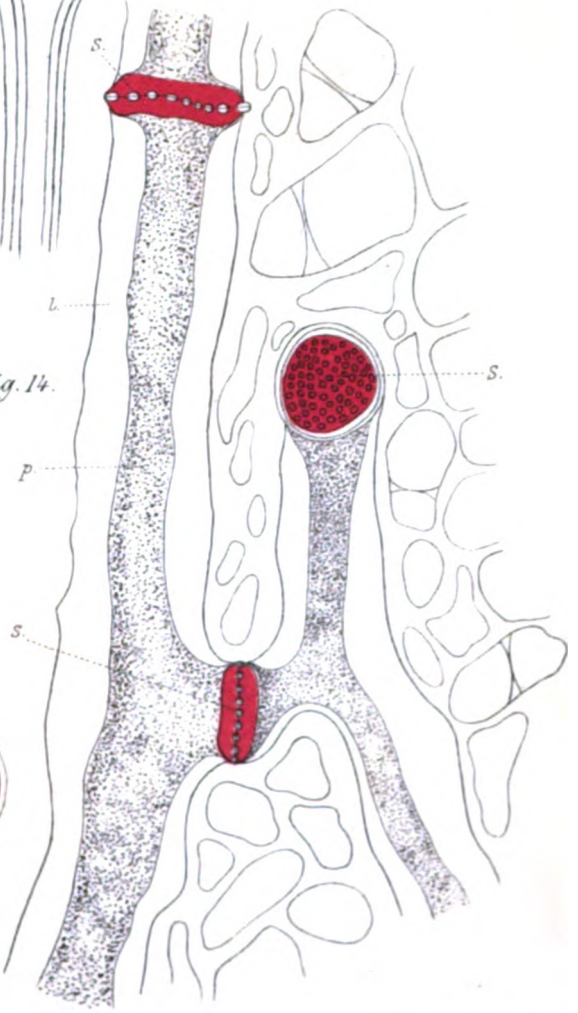

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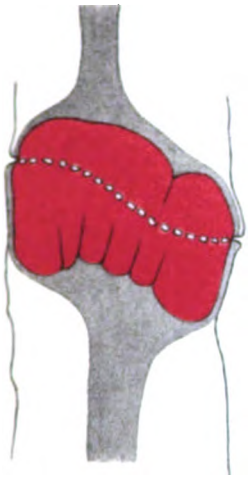
Fig. 15.



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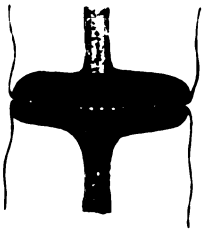
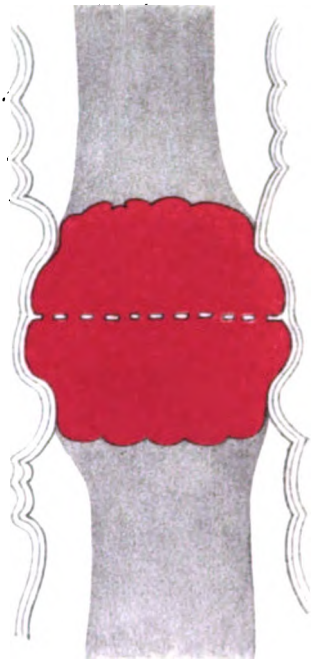


Fig. 17.



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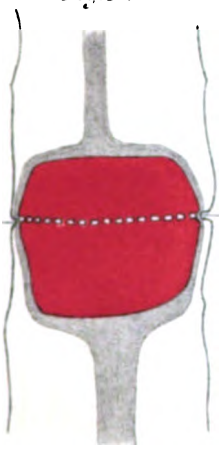
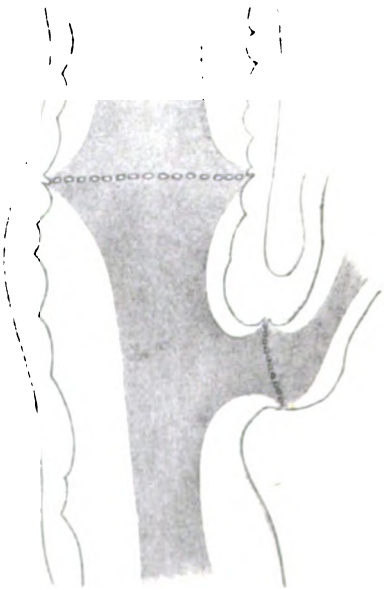


Fig. 20.



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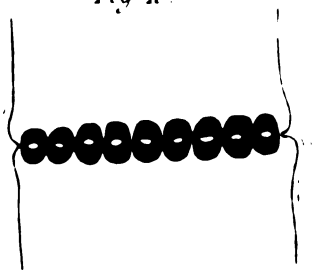

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OLIVER — OBLITERATION OF SIEVE-TUBES IN LAMINARIEÆ.

Fig. 13. *Macrocystis pyrifera.* Complex arrangement of branched trumpet-hyphae. (× 750.)

Fig. 14. *Macrocystis pyrifera.* Longitudinal radial section of the true sieve-tubes, showing three sieve-plates in three different planes. *S.* the sieve-plates, all of which are callous. The callus is drawn in red, *l.* lumen of sieve-tube between the wall and the contracted contents, *p.* (× 300.)

Figs. 15, 16. *Macrocystis pyrifera.* Much magnified views of fully developed callus-plates on the sieve-plates. 15 shows still a number of depressions and striae which represent the perforations so far as they survive; in 16 they are no longer visible. (× 450.)

Fig. 17. *Macrocystis planicaulis.* Showing a very typical adult callus-plate in this species. (× 550.)

Fig. 18. *Macrocystis Orbignyana.* Showing a callus-plate with curious irregular appendage, which might point to the callus being deposited by the protoplasm. (× 400.)

Fig. 19. *Macrocystis Orbignyana.* Early stage in the development of callus in a true sieve-tube. It arises over the cellulose-framework of the sieve-plate. The perforations are still quite open. The protoplasm is not drawn in. (× 570.)

Fig. 20. *Nereocystis Lütkeana.* Showing a true sieve-tube from a young specimen before the appearance of callus. (× 500.)

Some words on the life-history of Lycopods[1].

BY

DR. MELCHIOR TREUB,

Director of the Botanic Garden, Buitenzorg, Java.

THE results of recent investigation of the life-history of Lycopods have been made known to English readers in the columns of 'Nature' by Mr. Thiselton Dyer and by Professor Orpen Bower.

In his article concerning my own researches, an article of which I would only say that in it the author speaks too well of my work, Professor Bower points out, as an interesting result of the newer investigations on the subject, the great differences in the sexual generation of plants belonging to the same genus, *Lycopodium*. These differences can be explained in a small degree only by the different conditions under which the prothalli live, an opinion expressed also by Professor Goebel in his recent paper on *Lycopodium inundatum*, and this being so, it is necessary to study the development of as many species of *Lycopodium* as possible, in order to get a natural classification of the forms belonging to the genus.

In the other Vascular Cryptogams the classification has been based on the asexual generation alone; not because the other generation is not to be found or is not sufficiently known, but because it presents in the same genus and even in the same order only small deviations from a common type. In the case of Lycopods, I am inclined to think that a systematic arrangement, based on the asexual generation

[1] Read at the Manchester meeting of the British Association for the Advancement of Science in September, 1887.

[Annals of Botany, Vol. I. No. II. November 1887.]

alone, will prove to be rather a preliminary sifting than a natural classification.

At the present time we know three types of Lycopod-prothalli; 1, the *annotinum*-type, not sufficiently known; 2, the *cernuum*-type; 3, the *Phlegmaria*-type.

In four species of *Lycopodium*, which have not been hitherto studied, I can now give a brief account of the prothalli; three of them belong to the Phlegmaria-type, and the fourth to the cernuum-type.

The prothallus of *Lycopodium carinatum*, Desv., is exactly like that of *L. Phlegmaria*. Although I have been able to study a great number of prothalli of *L. carinatum*, I have not found any important difference between the sexual generations of these two species. As far as I have seen, the development of the embryo in *L. carinatum* is quite similar to what I found in *L. Phlegmaria*.

Of the species *L. Hippuris*, Desv., and *L. nummulariæfolium*, Blume, I have only had the opportunity of studying a few prothalli, because they are exceedingly difficult to get, though for different reasons. The prothalli of *L. Hippuris* seem to be very rare, at least in the western part of Java. Only three or four times have I found parts of a prothallus in connection with a young plant. They proved to be of the Phlegmaria-type, but they are much larger and thicker than those of *L. Phlegmaria*. Regarding the asexual generation, it may be worth while to notice that the suspensor seems to be generally very large.

In the case of *L. nummulariæfolium* the difficulty in finding prothalli has another cause. I do not think the prothalli of this species are very rare; but they are so thin that they can scarcely be detected upon their substratum, the dead layers of the bark of trees. Still there is no doubt they belong to the Phlegmaria-type. I have succeeded in raising from the spores, in the Buitenzorg laboratory, the prothalli of a form of Lycopod, nearly allied to *L. cernuum*, L., and to *L. densum*, Labill. Certainly the plant is not a variety of *L. cernuum*; it may be that it belongs to *L. densum*; but I incline to consider

the form as a new species. The prothalli have been cultivated on peat up to the formation of archegonia. For the detailed description of the sexual generation of this Lycopod, I beg to refer to a forthcoming number of the Annals of the Buitenzorg Garden. It will suffice to say only a few words here.

The prothallus belongs to the cernuum-type, still it differs more from the prothallus of *L. cernuum* than that of *L. inundatum* as known by the researches of Professor Goebel. The germinating spore begins by forming a globular body, what I have called the 'tubercule primaire,' in the prothallus of *L. cernuum.* Generally after a certain period of rest, several thin branches or filaments are projected from this 'tubercule primaire.' As a rule one of these branches thickens, afterwards continues its growth, and produces the sexual organs. Foliaceous lobes, like those produced on the apex of the prothalli of *L. cernuum* and *L. inundatum*, are not formed here. In a few instances very small prominences on the top of the prothallus might be considered as beginnings of rudimentary lobes.

Attempts to germinate spores of *L. curvatum*, Sw., a plant still considered by me as a distinct species, have not been successful until now. A few days after having been sown, the spores began to form small 'tubercules primaires.' These organs kept alive for eight or ten months in my laboratory, but could not be induced to protrude filaments and did not continue their growth.

There is another more general, and I should say more interesting, point of view from which Lycopod life-history may be considered. I mean the bearings of the investigations in the subject upon our views regarding the transitions between different groups of Cryptogams. Being still convinced that I have not attached too much value to these theoretical considerations, I am sorry I must confess that what I have briefly said on the four species newly investigated does not add very much to the principal facts already known.

In future parts of my 'Etudes sur les Lycopodiacées' I hope to give information of greater theoretical value. One

of the first things wanted is the complete embryology of *Lycopodium cernuum* or of an allied form. An exact knowledge of the development of this embryo is particularly required, after the publication of Professor Bower's interesting memoir on *Phylloglossum Drummondii*. Professor Bower's comparison of the adult *Phylloglossum* with the young Lycopod, a theoretical view expressed also by Mr. Bertrand of Lille, may find new support as soon as the embryology of *L. cernuum* is completely known. Last year I collected upwards of a hundred prothalli of *L. cernuum* in order to continue my researches on the embryo, but I was unsuccessful. The form of these prothalli makes the investigation of the embryo-development exceedingly difficult. I intend to try again as soon as I return to Java. Perhaps the prothalli I have described of the form allied to *L. densum* will give a better chance of success.

A second point to be investigated is the mode of vegetative propagation of *L. cernuum*. In this species the root-tops change into propagating organs of a remarkable form. These root-gemmae or bulbs produce on germinating young plants very much like those which come forth from prothalli. For several reasons I anticipate that the study of these gemmae, their formation and germination, will give interesting results. I have collected a sufficient amount of material during the last two years, and before long I hope to work out this subject.

A third desideratum is knowledge of the prothallus of *Psilotum*. It is to be feared this will remain a desideratum for a very long time. Although I have trained myself in finding young plants and prothalli of Lycopodiaceae in the forests, and especially on trees, I have never succeeded with *Psilotum*, although there are parts of our Java forests where *Psilotum flaccidum*, Wall., is not at all rare. After all, it is not impossible that prothalli of Psilotum are nowadays nowhere to be found, Count de Solms-Laubach's researches having made known the existence of organs, bulbils or gemmae, propagating the asexual generation of *Psilotum* even in European hothouses.

I may be allowed I think to say that the study of the Lycopodiaceae has been, for some time, somewhat neglected; yet this order may perhaps claim the honour of being one of the most important of all the Vascular Cryptogams. In one of Professor Williamson's remarkable memoirs 'On the organization of the Fossil Plants of the Coal-measures,' the learned Professor points out the relation between gymnospermous and lycopodiaceous plants of epochs long ago. On the other hand, the still existing Lycopodiaceae, poor remnants of an older age, have more points of resemblance with lower Cryptogams, especially Muscineae, than appears at first sight; and it may be that these Lycopodiaceae are the most interesting of the living forms of which we have not yet complete knowledge. I do not consider it at all impossible that there are still alive, for instance in the forests of Celebes or New-Guinea, forms whose *asexual generation* is not only smaller but morphologically much more reduced than *Phylloglossum*, and whose *sexual generation* on the contrary has a higher morphological differentiation than the prothallus of *Lycopodium Phlegmaria*.

On the modes of climbing in the genus Calamus.

BY

F. O. BOWER, D.Sc.,

Regius Professor of Botany in the University of Glasgow.

With Woodcuts 1-3.

THE genus *Calamus*, belonging to the family of Palms, must be well known to those who have visited Eastern tropical jungles. The stems, which are long and very tenacious, constitute the 'ratan cane' of commerce: they straggle through and over the other vegetation, the pliant shoot supporting itself by means of sharp reflexed prickles which present serious obstacles to the traveller. The growth of these plants is so dense and their prickles are so sharp that the Kandyan kings are recorded to have planted a fence of *Calamus* and other prickly climbers round their frontier forests, to which they trusted as a protection for their territory from the attacks of other native tribes[1]. These reflexed prickles are distributed over the shoot generally, but are largest, both in number and size, on special flagella, which project like whips over or among the surrounding growth of other plants, and after swaying freely in the wind for a time, hook on to stems, leaves, or even roughnesses of the bark of other plants, thus yielding an efficient support to the shoot which bears them[2].

A superficial observation of the plants of this genus shows that the flagella are of two kinds, differing in their

[1] See Emerson Tennent, Ceylon, vol. i. p. 108.

[2] Compare Treub, Annales du Jardin botanique de Buitenzorg, vol. iii. 2me partie, p. 172.

[Annals of Botany, Vol. I. No. II. November 1887.]

position and mode of origin on the shoot; also, that one or other of these is constant for different species; in fact, the whole genus may be divided into two sections according to the character of the flagella. These are in the one case the result of a simple extension of the apex of the phyllopodium (or 'midrib' of the leaf), as a long whip-like organ, covered, especially on the lower concave surface, with the reflexed prickles above mentioned. There is here no displacement of the parts of the shoot; in the mature state leaves and axillary buds follow in the ordinary succession[1]. In the second case, however, the flagella, though similar in general appearance to those above described, are found attached to the outer surface of the sheathing portions of the leaves, which themselves show no excurrent midrib (Fig. 1)[2]. The question arises, what is the morphological character of the flagellum in this second case?

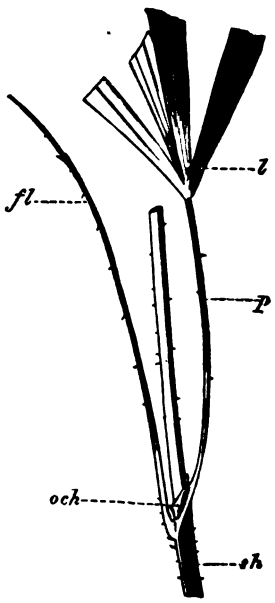

Fig. 1. Portion of shoot of *Calamus sp.*, half natural size, showing the lamina *l*, petiole *p*, sheath *sh*, ochrea *och* of the leaf; the flagellum *fl*, which is cut short, is inserted near the upper limit of the sheath.

In the large majority of specimens the attachment of the mature flagellum is near the upper limit of the sheathing portion of one of the leaves, and on its outer surface (Fig. 1); its median plane (i. e. the vertical plane including it and the main axis) forms an angle of divergence of about two-fifths with the

[1] An illustration of this type in *C. adspersus*, Bl., is given in Engler and Prantl, Die natürlichen Pflanzenfamilien, II Teil, 3 Abteilung, Fig. 14.

[2] The specific distinctions in the genus *Calamus* are well known for their difficulty: the material for this work was collected chiefly from plants which were neither in flower nor in fruit, and accordingly the specific names are not given.

median plane of the leaf, on the sheath of which it is inserted: the angle of divergence of the successive leaves is approximately two-fifths. Tracing the sheath downwards from the point of insertion of the flagellum to the next lower leaf, a projecting rib will be found to pass vertically downwards to its axil, and thus the median plane of the flagellum coincides with the median plane of the next lower leaf. From these facts it may be presumed that the flagellum is an axillary bud, and that in the course of development of the shoot it has become displaced, and has become adherent to the sheath of

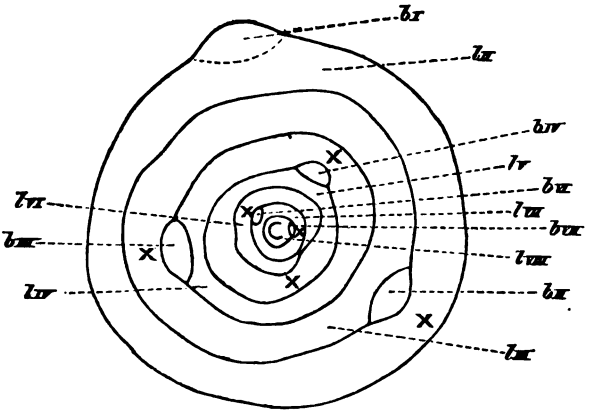

Fig. 2. Transverse section through a bud of *Calamus sp.* showing seven leaves (l^{II}—l^{VIII}): the midrib of each is marked thus ×: opposite each midrib, excepting those of l^{V} and l^{VIII}, is seen an axillary bud (b^{II}—b^{VII}): the outermost bud (b^{I}) is the axillary bud of the next outer leaf, which has been removed. (× 20.)

the next higher leaf[1]. There are abundant grounds, in addition to those above stated, for considering this to be the true interpretation of the case; they are as follows:—

(*a*) An examination of the adherent flagellum shows that it bears greatly reduced sheathing leaves, which, though they

[1] This assumption has been made by Drude; see Schenk's Handbuch, vol. i. p. 665. Treub, in describing them, calls them 'spadices metamorphosés.' See Ann. du Jard. bot. de Buitenzorg, vol. iii. p. 172.

produce no lamina, are still similar in character to those of the normal shoot.

(*b*) The inflorescences, when present, are produced on these flagella as axillary buds (cf. Die natürlichen Pflanzenfamilien, II Teil, 3 Abteilung, p. 16, Fig. 14, L).

(*c*) The displacement is sometimes only comparatively slight, whereas in most cases the flagella are inserted near the upper limit of the sheath. Examples are occasionally to be found (especially in young shoots) where the flagellum is almost exactly in the normal position in the axil of the lower leaf.

(*d*) In those shoots in which the displacement is greatest, an examination of the apical bud shows that the original position of the flagellum is axillary, and that the displacement is due to irregularities of secondary growth. If thick transverse sections be cut from such a bud (Fig. 2), the successive leaves may be seen as complete circles of almost uniform thickness all round: axillary buds are not always formed in their axils, but in those cases where they are present, the midrib of the leaf (marked × in Fig. 2) is usually seen to be the thinnest part; opposite it is to be seen the axillary bud, which may be recognised as being adherent, even in very early stages of development, to the next inner or higher leaf. In longitudinal sections through an apical bud (Fig. 3), when the next lower leaf is cut in a median plane, the base of its sheath is seen to be very thin, while opposite it is the axillary bud, which may be seen even in a very early state to be adherent to the next

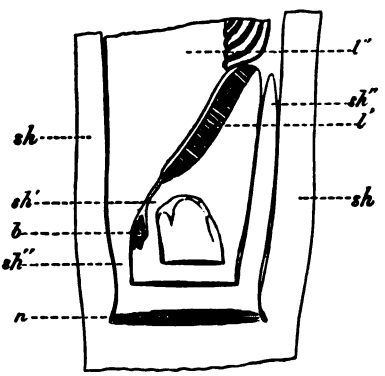

Fig. 3. Longitudinal section through a bud of *Calamus sp.*; l^{I}, l^{II} laminae; *sh*, sh^{I}, sh^{II} sheaths of corresponding leaves; *n* node; *b* bud in the axil of l^{II}, and already adherent to sheath of l^{I}. (× 10).

higher leaf. Thus, from observations of early stages of development, support is obtained of the view that the flagellum is a displaced axillary bud.

(*e*) Anatomical investigation also points in the same direction, though it would be unwise to regard this as more than secondary evidence. Transverse sections through the leaf-sheath below the point of insertion of the flagellum show that there is continued downwards into the leaf-sheath a sheaf of collateral bundles of the usual Palm-type, arranged with their protoxylem directed towards a central point, just as is the case in an ordinary stem: they are partially enclosed by a broad band of sclerenchyma, which serves as a barrier between the bundles descending from the bud, and those of the leaf on which it is inserted. Thus, taking the anatomical evidence for what it is worth, it also points in the direction above indicated.

On the above grounds it is concluded that in the second case the flagellum of *Calamus* is to be regarded as an axillary bud, which has been so far displaced as to assume a position adherent to the outer surface of the sheath of the next higher leaf.

Adhesions of members of one category to those of another are not uncommon, especially in connection with the inflorescence; thus, the axillary bud and subtending leaf may adhere together (inflorescences of *Tilia*, *Ruta*, and of many *Solanaceae*, &c.); or the axillary bud may be adherent to the main axis (inflorescence of *Ruta*, and of *Solanum nigrum* and *S. Dulcamara*, buds of species of *Juglans*, &c.). But in this case of *Calamus* a whole internode is overleapt, and the adhesion of the axillary bud is not merely to the internode, but even to the outer (lower) surface of the sheath of the next higher leaf. A near parallel to this is to be found in *Erythrochiton hypophyllanthus*, a Rutaceous plant, from New Grenada[1]: here the flowers are always produced at the back of the leaf, being

[1] Bot. Mag. 3rd Series, No. 303, Plate 5824. My attention was drawn to this remarkable plant by Professor Dickson.

inserted on the midrib sometimes at a point not far above the petiole, sometimes further up the lamina: the flowers, one to three in number, are shortly pedunculate, and are often subtended by a second leaf, the upper surface of which faces the back of that from which they both spring. The above account is taken from the Botanical Magazine; and, in default of actual specimens for observation or of any observations on the development, it seems not improbable that this peculiarity in *Erythrochiton* is due to a displacement similar to that above described in *Calamus*.

It may now be considered how the displacement of the axillary bud affects the plant as a whole. It is of the greatest importance to this, as to other climbing plants, that the assimilating leaves should be exposed to the sunlight, and this they strive to effect by a straggling habit, and by the help of adaptation for mechanical support on other plants, which allows them meanwhile to economise in the substances required for building up a rigid stem; the more efficient the mode of climbing the more successful will be the economy. If in the case of *Calamus* the axillary bud were developed as a flagellum, but remained inserted in the axil of the next lower leaf, the two members, being extended in the same plane and the leaf being the lower, it is improbable that the lower portions of the flagellum would come in contact with any support, since the leaf-stalk would be in the way, and the pressure upon a support as the plant straggled over the surrounding vegetation would certainly come first upon the leaf-stalk: in this case it would only be the upper portion of the flagellum which would be practically of use as a supporting organ. But the case is otherwise when the axillary bud is displaced and adherent to the sheath of the next higher leaf: it is thus clear of its own subtending leaf, and projects freely from the shoot at a point considerably above it. This being so, it is probable that as the plant straggles through and over the surrounding vegetation even the lower parts of the flagellum will have an opportunity of affording support to the whole shoot. Again, the angle of divergence between the displaced axillary bud

and the leaf to which it is adherent is about $\frac{1}{2}$, so that for all practical purposes the two are nearly opposite. If then the shoot of *Calamus* in straggling over other plants comes to rest in a forked branch, these opposite outgrowths would catch upon the fork, and serve as a support, just as in various plants divaricating branches (*Lantana*, *Pisonia*, etc.) or thorns (*Carissa*) serve the same end. Thus the displacement of the axillary bud is in this case to be regarded as an adaptation of the development of the shoot to meet the immediate needs of the plant.

Finally, the two sections of the genus show two very distinct types of adaptation of the shoot to meet the exigencies of a climbing habit: the one developes the apex of the leaf, the other the axillary bud as a flagellum.* Thus we see once again how plastic is the vegetative shoot in its mode of development within a single genus; or, in other words, how variable within a narrow circle of affinity may be the localisation of intercalary growth in shoots which correspond closely to one another in the origin and primary arrangement of the constituent parts.

On the limits of the use of the terms 'Phyllome' and 'Caulome.'

A SUGGESTION,

BY

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Regius Professor of Botany in the University of Glasgow.

IN the 'Practical Course of Instruction in Botany,' Part II, page 1, I appended a foot-note to the description of the leafy shoot of *Polytrichum commune*, which runs as follows:—'Though the terms "stem" and "leaf" are used here, it must be distinctly borne in mind that the members thus named, being parts of the oophore generation, are not homologous with, but at most only analogous to the stem and leaf in vascular plants, which are parts of the sporophore generation.' Thinking that this point would be generally admitted, no further explanation was given, and it was with some surprise that I found this passage objected to by certain of my colleagues. Since the point is not universally agreed to, and since this passage stands in a somewhat dogmatic form in a text-book designed for the use of students, the best course will be to state more fully the grounds upon which the statement is based. Moreover, there is at present a wave of what may be called 'morphological scepticism' passing over the minds of many in this country. Some think the distinction of the categories of members is not sufficiently definite; others are inclined to deny that distinctions can be drawn at all; thus the present appears to be an opportune time for the consideration of the basis on which we rest our distinction of the parts of the shoot, viz., stem and leaf, and the limits which may, and I think should, now be placed on the application of

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those terms. If, in pursuing this subject, I traverse ground which is too familiar for the taste of some, the excuse will be that this is done in the interest of clearness.

Sachs has stated in his Lectures[1] that 'it is impossible to express morphological ideas clearly and exhaustively by means of simple definitions.' Since the definitions cannot be simple, it is all the more necessary to be aware of, and to estimate at their true value in relation to one another, those criteria upon which organographical distinctions are, or have been, based; these will now be considered seriatim, and with special reference to the distinction of the parts of the shoot, viz., axis and leaf.

I. The first basis of distinction of the parts of plants was undoubtedly that of *external form and appearance*, and it is also popularly used to the present day by the lay public, which would call underground stems roots, and the phylloclades of *Ruscus* leaves. It is unnecessary here to show that the external form and appearance of the mature member form an insufficient basis for morphological distinction, since this principle is insisted on in every text-book.

II. Nor is it necessary here to point out, or prove by examples, that *function* is an unsafe guide. It may, however, be noted in passing, that function has been made the chief basis of the system of physiological organography propounded by Professor Sachs in his Lectures; and though he expressly states that his system is not intended to replace purely formal morphology, there can be little doubt that his use of familiar terms in a new sense will tend to obscure their morphological meaning in the minds of many.

III. A method of distinction of members according to the disposition of the tissues in the mature state (the *anatomical method*) is one which has especially met with acceptance in France, where it took its origin and was first developed in the extensive researches of Van Tieghem[2]. This author

[1] Engl. Ed. p. 2.

[2] Recherches sur la Symétrie de Structure des Plantes Vasculaires, in Ann. Sci. Nat., sér. 5, t. xiii.

wrote, with special reference to the leaf[1], as follows: 'We shall show that in the whole series of vascular plants all the bundles of the leaf are in their disposition and orientation placed with reference to a plane which includes the axis of symmetry of the stem and the radius of insertion;' and continues, 'thus while the plant-axis in both parts, viz., root and stem, which compose it, is throughout symmetrical with reference to a line, the appendage is only symmetrical with reference to a plane.' This method of distinction, which its author applied to the solution of various morphological problems in connection with the flower, was taken up and further elaborated, and still more precisely stated by Bertrand[2]; and if the constancy of structure of corresponding members of all vascular plants were greater than it is, the anatomical method might doubtless prove a ready and efficient rule of thumb for distinguishing different categories of members and solving morphological problems. Unfortunately numerous known facts are against this: it will be well to cite a few pregnant exceptions to the rules as above laid down, and these are to be found especially in shoots of peculiar conformation.

In various species of *Juncus* a foliage leaf projects beyond the apparently lateral inflorescence as an elongated conical or nearly cylindrical structure, which shows just above the inflorescence a sheathing base; if transverse sections of this, which is actually a leaf, be examined, those cut through the sheathing portion show an arrangement of the tissues which would fall under Van Tieghem's definition of a leaf; but in the

[1] We need not here refer to the anatomical distinction of stem and root, since we are at present specially concerned with the leaf. It is, however, to be noted that Van Tieghem began his researches on the root, which is much less subject to metamorphosis than stem or leaf, and it might accordingly be expected that its type of structure would be more uniform than theirs; he found but few roots of aberrant structure. His researches on the stem and leaf have, I believe, never been completed, and in his Traité de Botanique he lays no great stress upon the anatomical method of distinction of parts of the shoot. It may perhaps be concluded from this that he has not found the anatomical method apply so readily to the more plastic members of the shoot as it does to the more uniformly constructed root-system.

[2] Archives Botaniques du Nord de la France, 1881.

cylindrical upper portion the structure is symmetrical round a central point, and even corresponds in detail to that of the axis below the inflorescence. Accordingly the upper portion of the leaf would, on anatomical grounds, fall under the definition of an axis. Thus one and the same member, which on other grounds is regarded as a leaf, shows in its lower portion those anatomical characters which are ascribed to the leaf, in its upper portion those ascribed to the axis[1]. The tubular leaves of species of *Allium* present similar difficulties, the sheathing lower portion conforming to the foliage type, while the tubular upper portion has the vascular bundles corresponding in position and arrangement to the type of the stem. Again, in the ensiform leaves of *Iris*, *Tofieldia*, etc., and the phyllodes of certain *Acacias*, it would be impossible to tell from the transverse section alone, and judging by the arrangement and orientation of the bundles, whether the member were a leaf or an axis.

The exact converse of the case of *Juncus* or *Allium* is shown in the phylloclades of *Ruscus androgynus*[2]. If transverse sections be cut at the base of the phylloclade, the arrangement and orientation of the vascular bundles is according to Van Tieghem's type for an axis, being symmetrical with reference to a central line; but if sections be cut successively further from the base, it will be seen that the arrangement and orientation of the bundles gradually passes over into Van Tieghem's type for the leaf. As Professor Dickson has pointed out, the phylloclade undergoes a twist at the base, so that the morphologically lower surface is directed upwards, and this actually upper surface bears no stomata, though they are to be found in large numbers on the morphologically upper but downward directed surface; all the vascular bundles have their xylem directed upwards, i.e. towards the morphologically lower surface. In passing from the base where the

[1] This example has been cited by Goebel as showing that the distinction of members on anatomical grounds is untenable. Vergl. Entw., p. 128.

[2] The structure of these is described by Professor Dickson (Foliage Leaves in *Ruscus androgynus*) in Trans. Bot. Soc. Edin., vol. xvi.

arrangement is characteristic of the stem, to the upper expanded portion where the structure of tissues and orientation of bundles is throughout characteristically foliar, the bundles first separate into groups, each group having as its centre a relatively large bundle, which is so placed that the xylem is directed towards that surface (the morphologically lower) which is ultimately directed upwards, and the smaller irregularly arranged bundles then coalesce with the larger one. Thus we have here the converse case of a member, which on other grounds would be recognised as an axis, showing in its lower portion an axial type of internal structure, which gradually changes in its upper portion to that laid down by Van Tieghem as characteristically foliar.

Though other examples might be adduced, these will suffice to show that morphological distinctions of the parts of the shoot cannot be based on the disposition or orientation of the vascular bundles: equally insecure would be conclusions based upon their number, as is obvious when it is remembered that scale-leaves are often without vascular bundles at all, and that the cotyledon of *Lycopodium* may show a similar simplicity of structure[1]; also the case of the genus *Gnetum* may be cited, in which I have already shown[2] that in one species (*G. africanum*) the central bundle, which is present in other species, is absent, though there is no corresponding difference of configuration. And lastly, observations on the point of fusion of vascular bundles from one member with those of another give only uncertain ground for morphological conclusions, since we know that in cases where there is no question of morphological character the fusions may take place at very irregular points (e.g. the shoot of *Helianthus*).

From the examples above quoted (and they might be greatly added to) it appears that observations of the arrangement, orientation, number, or point of fusion of vascular bundles constitute an insufficient foundation for the solution

[1] Treub, Ann. Jard. Bot. Buit. vol. iv. p. 134, in *L. cernuum*. Goebel, in Bot. Zeit., 1887, in *L. inundatum*.

[2] Phil. Trans., 1884, Part ii. p. 599.

of morphological problems, and it will be noted that the anatomical method breaks down most conspicuously at the very points where questions of the nature of members arise, that is, where there is some marked peculiarity of external conformation. But it is not necessary on this account to throw anatomical evidence entirely on one side; it may be taken advantage of as collateral evidence to support a view based on other and firmer ground; still, since it is plain that the internal structure follows in great measure the modifications of external form and function, observations in this direction can never acquire first-rate morphological importance[1].

IV. Passing now from the consideration of the mature member, upon the characters of which it is found impossible to base a consistent distinction of members of different categories, to their origin and development, we may consider how observations on these points have been, or are used as a basis of classification of members. It was Schleiden who first laid special stress on development as the basis of morphology[2]; and though his proposed distinction of axis and leaf *according to the duration of apical growth* is not now found sufficient, his service to the science in turning attention to development should not be underrated. His definition is as follows[3]:—'So ist also das Blatt die aus der Grundlage der Pflanze, der im Wachsthum und daher morphologisch unbeschränkten Axe, hervorgehende, im Wachsthum und daher morphologisch beschränkte Form; unter diesen Begriff fallen alle Blattorgane, und alle Axen sind ausgeschlossen.' Though this distinction holds for the large majority of cases, still since stems of limited growth are known to exist (e.g. *Welwitschia*, species of *Streptocarpus*, the receptacle of Compositae, various

[1] Hofmeister, All. Morph., p. 415, states broadly, 'Uebereinstimmungen oder Differenzen der äusseren Form, des inneren Baues, der Function sind nicht Maassgebend für die Deutung eines gegebenen Gebildes als Achse, Blatt, oder Haar.' He does not, however, give examples from vascular plants, which would bear out this statement as regards the internal structure.

[2] Grundzüge der Wiss. Botanik, p. 20: 'Die Grundlage für alle specielle botanische Morphologie ist die Entwickelungsgeschichte.'

[3] Grundzüge, p. 172.

thorns, etc.), while leaves have not unfrequently a very extensive and apparently unlimited apical growth (e.g. *Lygodium*, *Gleichenia*, etc.), this distinction between axis and leaf cannot be maintained. Nevertheless, the fact that the leaf is usually limited in its apical growth is to be noted as one of the distinctive though variable characters of the leaf.

V. According to the number of layers of meristem which give rise to them respectively, a general difference may be traced between leaves and lateral axes. Upon the value of this evidence it will be best to quote from Warming, who has made such fine and extensive observations in this direction[1]. He writes: 'It is impossible to separate phyllomes and caulomes by constant morphological and genetic characters. We have seen in the second part that they arise from the same peripheral tissue, but at slightly different depths: the leaves spring generally from the first and third layers of the periblem, the weaker leaves, such as the bracts in many inflorescences, even from the first layer only; stems hardly ever originate in the first layer, but most frequently in the third or fourth. This character has its importance, and may often serve as a criterion for determining the nature of an organ of doubtful morphological character .... but of course it must not be regarded as an absolute index, which should always be decisive. I think we should rather consider it as a circumstance which is intimately connected with the size of the organs and the space which they require: the more vigorous they are, and the more permanent the rôle which they are destined to play, the more space they require and the deeper is their origin in the axis; since caulomes, by reason of their biological rôle, almost always require more space and vigour, they also originate at a greater depth.'

VI. We may next consider the criteria of *relative time and place of origin*, these being adopted by Hofmeister as his basis of distinction of lateral axis, leaf, and hair[2]: he

[1] Recherches sur la ramification des Phanerogames, in Forgreningsforhold, French résumé, p. xvii.

[2] Allgemeine Morphologie, p. 411.

wrote as follows: 'Lateral axes, leaves, and hairs, arrange themselves as regards the time and place of their appearance according to their rank. New lateral axes rise from the surface of the growing-point earlier, and nearer to its apex than the youngest rudiments of leaves.' Against this is to be set the statement of Sachs[1]: 'I constantly find in vegetative shoots and many inflorescences of Phanerogams young leaves above the youngest axillary buds.' This question has also been treated at length by Warming[2], who has shown that though in the vegetative shoot the leaf as a rule precedes the axillary bud, in many inflorescences the bud may precede its subtending leaf, or the subtending leaf may be entirely absent. Again, Goebel's observations[3] on 'dorsiventral inflorescences' and on 'intercalary growing-points' indicate, together with the above, that relative time and place of origin will not serve as a safe criterion of distinction of axis and leaf. In fact we arrive at the conclusion put forward by various writers, that all the above-mentioned characters have only a relative value as applied to the distinction of axis and leaf, all of them being limited by exceptions: in other words, organic nature is not limited by strict rules, and a perfectly natural system of morphology of the shoot cannot be based on narrow definitions.

The difficulty of defining and distinguishing stem and leaf is in itself to be regarded as a strong justification of their designation under the common term 'shoot,' which Sachs has adopted in his Lectures as the correlative of the 'root.' Accepting this idea of the shoot as a whole, one is apt to doubt, in view of the difficulty of their definition, whether there be any essential difference between axis and leaf; and this question is closely connected with the idea of a possible 'terminal leaf:' if there be any recognisable difference then the terminal leaf is at least a possibility. Now Sachs'

[1] Textbook, 1st English edition, p. 154, footnote.

[2] Forgreningsforhold, pp. viii–xi.

[3] Ueber die Verzweigung dorsiventrale Sprosse. Also Vergl. Entwickelungsgeschichte.

well-known definition of stem and leaf is as follows[1]: 'Stem (Caulome) is merely that which bears leaves; Leaf (Phyllome) is only that which is produced on an axial structure in the manner described in paragraphs 1–7:' and he proceeds to say 'that which is common to all leaves is their relation to the stem.' How then about the possible so-called 'terminal leaf'? can such a thing exist? On this point Goebel has written a remarkable passage which runs as follows[2]: 'Terminal leaves are unknown in the vegetative region, though this is but a statement of experience, which would be put aside by the first well-grounded exception; and doubtless a foliage-leaf would remain a foliage-leaf, even if it arose in a terminal position on the growing-point, but therewith the last developmental distinction between stem and leaf would disappear.' This implies that some other basis of distinction would remain, by which the leaf might still be recognised as leaf when terminal, and not merely as a development of the axis, which it would be according to Sachs' definition. What then is that distinction? The distinction, which Goebel would here recognise as overriding Sachs' definition, is one based on comparison of nearly allied forms (a phylogenetic distinction), or possibly of successive members of the same individual. If then the possibility of a 'terminal leaf' be admitted[3], the definition of Sachs appears to be an arbitrary one, and is not to be accepted as final. However, no actually 'terminal leaf,' in the sense above indicated, has been observed. What we require at present is a suitable nomenclature for what is actually seen in nature, and that based upon the definition of Sachs is the best hitherto proposed.

[1] Textbook, 1st English edition, p. 136.

[2] Vergleichende Entwickelungsgeschichte, p. 184.

[3] Compare Warming, l. c., p. xviii. Also Eichler, Blüthendiagramme, p. 48. This question would appear to have lost much of its interest and importance to those who accept Goebel's view of the sporangium as a member 'sui generis.' Beneath it, however, as indicated in the passage from Goebel above quoted, there lies a morphological principle, which is certain to acquire greater importance in the future.

Thus, there is another factor in the morphological problem beyond those above-mentioned, viz. the use of a comparison of closely allied forms, the results of which are accepted by some as overriding conclusions based on other grounds; and whether or not, in the present state of our knowledge, we are justified in regarding such comparison as of first-rate importance, we must take into account this which may be called the 'phylogenetic factor.' An ideal system of morphology of the shoot, which should recognise the true homologies of all members, their origin, and metamorphoses, would be one based on a full knowledge of phylogeny, and what there is of arbitrariness in Sachs' distinction is to be looked upon as a concession to the incompleteness of our knowledge on this point. How incomplete is our information and how uncertain our view, especially with regard to the descent of the Phanerogams, all must be aware. But though our knowledge in this direction is at present far too scanty to form a general basis for an exclusively phylogenetic system of classification of members, there are certain points in the whole series of plants at which it is certainly sufficient for drawing a broad distinction. We recognise that at various points in the series of plants 'parallel developments' have taken place. If our morphology is ever to have a phylogenetic basis, we shall do well not only to admit the fact of these parallel developments having taken place, but, where such a course will conduce to clearness of conception, distinguish them from one another in our nomenclature. It will be well to begin upon what is certainly the most clearly ascertained, as it is also the most prominent example of parallel development in the vegetable kingdom, viz. the foliar differentiation of the shoot in the sporophore, as well as in the oophore generation[1].

[1] While the terms 'root' and 'shoot' may be accepted, as correlative terms, in the general sense proposed by Sachs, and as including the corresponding parts of oophore and sporophore generations, it must be clearly borne in mind that the differentiation of such parts must have arisen in the two generations in just as independent a manner as the further differentiation of the shoot into axis and leaf; but there would be no sufficient advantage in marking this by a change of terminology to justify disturbing terms which have met with general acceptance in their

The evidence that such a parallel differentiation of the shoot has actually taken place is of the strongest possible kind, and is based primarily upon the researches of Hofmeister, by whom it was first demonstrated that the Moss-plant corresponds in its position in the life-cycle not to the Fern-plant, but to the Fern-prothallus. Taking first the sporophore generation in such a series of forms as *Coleochaete*, *Anthoceros*, *Phylloglossum*, a Fern, and a Phanerogam, we should in them see broadly indicated the rise of the sporophore generation; it is true the series is defective, the gap between the non-foliar sporophore of *Anthoceros* and the foliar one of *Phylloglossum* or of a Fern is a wide one; but there can be no reasonable room for doubt that the differentiation of the shoot into caulome and phyllome was a gradual one, though the intermediate forms have dropped out of existence. This view is strongly supported by analogy of the oophore; here, in such a series of types as *Pellia*, *Blasia*, a leafy *Jungermannia*, and a Moss, we have illustrated a similar but quite distinct differentiation of the shoot of the oophore generation; the two processes of differentiation, taking place at different points in the life-cycle, must necessarily have progressed independently of one another, and all the knowledge we possess of the plants concerned confirms this view[1]. Accordingly, notwithstanding the apparent similarity in external conformation, the 'leaf' in the oophore is not the lineal descendant of the leaf in the sporophore: thus we can only recognise the parts of the shoot in the sporophore and oophore generations as morphologically *analogous* to one another; the two are 'homoplastic,' but not morphologically homologous. This being so, I think it is desirable in the interests of clearness

present sense. The same may be said of the terms stem and leaf, which may still be accepted in a general sense as applicable to corresponding parts of oophore or sporophore generation.

[1] The notable fact of the similarity in external conformation of the oophore and young sporophore in *Lycopodium cernuum* and *inundatum* presents no obstacle to this view: it would appear that the differentiation had taken place both in oophore and sporophore, but still the process of differentiation might have been independent in the two generations.

and especially on behalf of students, that this conclusion should appear on the face of our terminology; the enclosure of the words 'leaf' and 'stem' in inverted commas, when applied to the oophore generation, is but an impotent distinguishing mark. I would therefore propose that the terms phyllome and caulome be reserved for those parts of the sporophore generation which are usually so called, thus retaining those terms in their original sense; while the terms 'phyllidium' and 'caulidium' might serve for the analogous developments in the oophore generation. Such a distinction of terms has been habitual in regard to the roots, the term 'root' (rhizome), in the sense adopted by Sachs in his Text-book, being applied to the true root of the sporophore, while the terms 'rhizoid,' 'rhizine' (or perhaps better 'rhizidium'), express the analogous and functionally similar parts in the oophore[1].

I am aware that objection will be raised to this proposal on the ground that it will be impossible to distinguish all parallel or morphologically analogous developments by distinct terms: thus, if we admit that heterospory has arisen at more than one point in the Vascular Cryptogams, it is at present unnecessary to distinguish the different sporangia in heterosporous Ferns, fossil Equisetums, and Lycopods by distinct terms: this is obvious. But it is, as far as I can see, no objection to the adoption of distinctive terms in what is the most prominent case of parallel development in the whole series of plants, or in other cases also where such a course would be conducive to clearness[2].

[1] It is in connection with the term 'rhizoid' that Professor Sachs has most conspicuously thrown overboard a distinction of terms which conveys the idea of want of homology in functionally similar parts. The avowed object of removing the cause of that 'prejudice against descriptive Botany still frequently existing even in scientific circles' can hardly be accepted as sufficient to justify the sacrifice of clearness of conception. Compare Lectures, p. 35.

[2] There can be few morphologists who have not felt the impropriety of designating by the same term the true leaf or phyllome of the higher plants and such members as the so-called leaves of *Nitella* or *Caulerpa*, the limited lateral branches of Florideae, the amphigastria of *Marchantia*, none of which can have been lineally connected with the true leaf of the sporophore: such members would fall under the term phyllidia, and thus be distinguished from the true sporophoric phyllome. It is true the analogies are at times extremely close, as that of the phyllidium of

Again, it may be urged that if this distinction, based on a want of homology, be marked by a difference of terms, the student will conclude that all those developments which are termed 'phyllome' or 'caulome' are lineally connected, and likewise all those called 'phyllidium' and 'caulidium': this difficulty would, however, be due to a process of defective reasoning from which the student must take care to guard himself. The fact is that it is not clearly desirable that every recognised case of want of homology of homoplastic members should be distinguished by definite terms, nor is our knowledge sufficient as yet to justify an extensive use of phylogeny in checking the nomenclature of morphology, even if it were desirable.

Again, it may be argued that observations of apogamy and apospory show that the two alternating generations are not so distinct from one another as has been supposed. This objection is virtually answered in another place[1], where the opinion is expressed that such observations as those of apospory do not indicate a reversion bearing a deep morphological meaning, but are rather to be regarded as mere sports.

In thus proposing to recognise more fully the fact of parallel development in the terminology of the science no new principle is made use of: it is merely intended to bring generally accepted conclusions into greater prominence, so as to obtain a clearer view. It is, however, a move exactly in the opposite direction to that recently made by Prof. Sachs. In his Lectures on the Physiology of Plants he brings together under a common name homoplastic organs of radically different origins[2]. Though this system of physiological organography is an undoubted advantage to the physiologist, who, in pursuing his special line of study, will necessarily centre his attention on the individual rather than on the race, the use of the old terms in a new sense, which disregards such conclusions as are based

Fissidens to the phyllome of *Iris* or *Narthecium*; but it is exactly in these cases that it is most necessary to keep clearly before the mind the fact that these members are not lineally related, but are only analogous to one another.

[1] Trans. Linn. Soc. vol. ii. p. 322. [2] Annals of Botany, vol. i. p. 84.

on a phylogenetic view, is little short of a disaster to comparative morphology. Notwithstanding Prof. Sachs' disavowal[1] of any wish to supersede or exclude purely formal comparison, the adoption of terms which have already a more or less definite morphological meaning in a different and still less definite physiological sense must result in confusion in the minds of students. Here again the regret may be expressed that in adopting a new point of view, in itself of the greatest value, a correspondingly new series of terms was not introduced. In morphology the phylogenetic factor is certain to become of constantly increasing importance as the effect of the hypothesis of evolution takes form in a sounder view of the relationship of the main groups of living plants: it is only to be expected that, as the sum of known facts increases, morphological distinctions based upon phylogenetic view will be more clearly recognised. The suggestion embodied in this paper, to limit the terms 'phyllome' and 'caulome' to the sporophore generation, is intended as a step in this direction. We should thus arrive at the following classification of vegetative members:—

I. Shoot { Stem { Phyllidium (oophore). / Phyllome (sporophore). } / Leaf { Caulidium (oophore). / Caulome (sporophore). }

II. Root . . . { Rhizidium or Rhizoid } (oophore). / { Rhizome or true root } (sporophore).

The terms shoot and root, stem and leaf, would thus be used in a general sense, being applicable to the corresponding parts in both oophore and sporophore indiscriminately; the terms phyllome, caulome, and rhizome would, however, be applied only to the parts of the sporophore, while the terms phyllidium, caulidium, rhizoid or rhizidium would be reserved for the corresponding parts of the oophore.

[1] Lectures, p. 72.

On the Absorption of Water and its relation to the constitution of the cell-wall in Mosses.

BY

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THE mode of absorption of water by Mosses has occasioned a certain amount of controversy. Haberlandt[1] maintains that his experiments have proved that water is absorbed by the parts of the moss-stem and root-hairs imbedded in the soil, and is transmitted thence through the aerial parts of the stem to the so-called leaves. This opinion he still adheres to in his latest paper on the subject[2].

Oltmanns[3] maintains, on the contrary, that water is absorbed in the oophyte of the Mosses by means of the leaves and that there is no transpiration-current. Oltmanns' experiments and the general considerations which he brings forward in support of his view are most convincing.

I was desirous, in connection with certain speculations as to the morphological relations of the Muscineae to the higher Cormophytes, of knowing which of these views is the right one, and therefore I determined to make some observations which should if possible settle the matter one way or another. I ought perhaps to state that when I began my observations I was distinctly biassed in favour of Haberlandt's view.

In beginning my observations there was one point which

[1] Haberlandt, G., Ueber die physiologische Funktion des Centralstranges im Laubmoosstämmchen, in Berichte der deutschen botan. Gesellschaft, Bd. I. (1883), p. 268.

[2] Haberlandt, G., Beiträge zur Anatomie und Physiologie der Laubmoose, in Pringsheim's Jahrbücher fur wissenschaftliche Botanik, Bd. XVII (1886).

[3] Oltmanns, F., Ueber die Wasserbewegung in der Moospflanzen und ihren Einfluss auf die Wasservertheilung im Boden, in Cohn's Beiträge zur Biologie der Pflanzen, Bd. IV, Hft. i. (1884).

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almost immediately caught my attention, namely, that whether in the wild state or under cultivation changes in the dampness of the air affected the oophyte much more rapidly than the sporophyte; so much so, that on quite hot dry summer days, when the leaves of the oophyte of Mosses, which were in fruit, were quite withered and rolled up with the drought, the sporogonium was quite fresh and did not wither unless the drought was excessive. It was, in fact, only very rarely, even in the past exceptionally dry summer, that I found the sporogonia of Mosses (that is, of course, those which had not dried up after maturation of spores) appreciably affected by the want of water. This observation and the rapidity with which the leaves of Mosses recover from the dried-up condition after a little rain or dew has fallen or formed upon them, suggested certain experiments.

I obtained stems of *Polytrichum commune*, L., some 15–20 cm. in length, which I placed with their cut ends in water, about half-an-inch being below the surface. Placed in a cool room with a dry atmosphere, in less than half-an-hour all the leaves, except the last half-dozen nearest the water, were withered. Some stems of *P. formosum*, Hedw., with their cut ends in a solution of eosin in water, were placed, some in an atmosphere just so damp that the leaves did not wither, others in a drier atmosphere so that the leaves withered slowly. In neither case did the eosin pass more than a few millimetres up the stem, about far enough to be accounted for by diffusion. If, on the other hand, water was placed on the leaves, or if one of the stems was dipped growing point foremost into water, the cut end being carefully kept dry, the leaves rapidly recovered. If, instead, the cut end of the stem was dipped into a solution of eosin in water, the leaves and tissues of the stem were found to be full of the solution. It then became clear that water can be absorbed by the leaves of the Moss, and consequently can pass through the external cell-walls of the leaf.

The subject of observation then became the constitution of the cell-walls of the leaves and stems of the oophyte

of the Moss. I chose *Polytrichum commune* for my observations as before, with the results given below stated for the stem; as the leaves gave the same results, these are not mentioned separately.

Transverse sections of stem of oophyte:—

Iodized zinc-chloride (*Schulze's solution*):—central strand of small-celled tissue only coloured *blue*, all the external tissues coloured *yellow*.

Caustic potash:—the cell-walls of the peripheral tissue remain brown and are not dissolved by boiling.

Aniline chloride:—the cell-walls of peripheral sterome lose their brown colour and become *yellow*.

Chromic acid, strong, but not quite concentrated:—rapidly dissolves all the cell-walls without leaving anything whatsoever except the protoplasmic contents of the cells which float about freely in the liquid; there is no trace of a cuticle to be found either on the leaves or stem.

Nitric acid and chlorate of potash (*Schulze's mixture*):—sections warmed in this mixture become completely colourless, and all the cell-walls give characteristic cellulose-reaction with iodized zinc-chloride, even the most external layer of all.

Nitric acid:—turns all the cell-walls of external tissues and those of the central strand orange yellow.

Hydrochloric acid:—turns cell-walls of peripheral tissues from yellow-brown to orange or red-brown, with purplish tint in some of the more external cell-walls.

Sulphuric acid, strong:—causes swelling more or less of cell-walls of all the tissues.

Carbolic acid:—turns peripheral tissues a very slight greenish tint.

In view of the ease with which water is absorbed at the surface of the leaves and stem of the oophyte of this Moss at least, and of the actions of the re-agents given above, it will, I think, be clear that there is no cuticularization of the cell-walls nor is there any cuticle present. From the action of some of the re-agents it is evident that the

easy by the external walls being slightly changed in such a way as to make their power of imbibition greater. This change appears to be similar to, if not identical with, ligneous change. As a result of this condition of the cell-walls, the leaves are the chief organs for absorbing water as well as for carrying on assimilation in the oophyte.

In the sporophyte the external cell-walls are not only cuticularized, but there is a distinct cuticle present, consequently water can only be absorbed normally at one point, by the foot which is inserted in the tissues of the oophyte; in experiment, of course it is absorbed at a cut surface. Since water can in the sporophyte only be absorbed at one point, there must be arrangements for conveying it to other parts. This is done as I have shown[1] by a transpiration-current which passes up the seta to the apophysis (the organ of assimilation), where transpiration takes place through the stomata.

[1] Vaizey, J. Reynolds, Note on the Transpiration of the Sporophore of the Musci, in Annals of Botany, Vol. I, No. 1 (1887).

ST. PETER'S COLLEGE CAMBRIDGE.

On the use of certain plants as Alexipharmics or Snake-bite Antidotes.

BY

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IN the department of Economic Botany considerable activity is displayed in investigations whereby the medicinal properties of plants may be more fully utilized. Numerous plants that once were shunned on account of their poisonous properties have of recent years been made subservient to the wants of man. A few instances of these may well be cited. The Umbsuli, a species of *Strophanthus* that yielded the arrow-poison of South Africa, is found of incalculable benefit in cardiac diseases. The celebrated Ordeal Bean of Old Calabar, *Physostigma venenosum*, Balf., a plant so deadly as to be ordered to be destroyed by the Government, has yielded under careful research a powerful sedative of the spinal cord. Another African ordeal poison was yielded by *Erythrophloeum guineense*, Don., the Sassy of the Gambia, and the Casa or Casca of the Congo. The bark yielded by infusion a 'red water,' and the ordeal was administered in this form. In medicine the drug is useful in the treatment of cardiac dropsy and passive hemorrhage. One of the most deadly plants in the West Indies, formerly used as a 'safe' poison by Obeah men, and probably still largely used in Hayti, is *Urechites sub-erecta*, Muell. Ang. Recently this plant has been recommended in the treatment of yellow fever. The Jamaica Dogwood, *Piscidia Erythrina*, L., chiefly used as a narcotic and as a fish poison,

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is much valued in the United States as an anodyne and hypnotic.

These are a few notable instances in which plants formerly used destructively against human life have been rendered serviceable in the treatment of disease. Researches in this direction are now being carried on with so much energy that there is little doubt many more plants will be found to possess properties now unknown.

As opposed to plants remarkable for their poisonous qualities, there are many which have gained a reputation as alexipharmics or counter-poisons. Of these there are two classes—those which are believed to be antidotes to animal poisons, and those which are looked upon as antidotes to the poison of other plants. These antidote-plants have so far received only partial attention. Information respecting many of them is only accessible in books of travel, and the accounts given are vague and unsatisfactory. The subject nevertheless is one of considerable interest, and it is felt that knowledge can only be extended by directing attention to these plants and presenting in a brief review what is at present known respecting them.

Of plants reputed to be useful as antidotes against the poison of other plants the number is by no means large.

A well-known cucurbitaceous plant in the West Indies, *Fevillea cordifolia*, L., is called Antidote Cacoon, because of its supposed virtue to expel the poison of the Cacoon (*Entada scandens*, Benth.). The fresh juice of *Oxalis corniculata*, L., is used to relieve the intoxication induced by *Datura* seeds. The Ordeal Bean of Calabar, itself a deadly poison, is nevertheless said to be useful in the treatment of strychnine-poisoning. The small roots of *Hernandia sonora*, L., are claimed to be 'a sure antidote against poison from poisoned arrows;' while the roots of *Cissampelos Pareira*, L., are an 'excellent antidote against all poisons.' The Manchioneel-tree (*Hippomane Mancinella*, L.) has been credited with characters so poisonous as to rival the celebrated Upas-tree, and the juice and tender buds of the White-wood Cedar

(*Tecoma leucoxylon*, Mart.) are stated to act as an antidote against the juice of the Manchioneel; in this case both the poison and the antidote are found to grow side by side.

Another antidote to the poison of the Manchioneel is derived from the uncooked rhizomes of the Arrow-root plant, *Maranta arundinacea*, Rosc. These possess in a fresh state acrid, rubefacient, and salivatory properties. When applied to a wounded surface caused by the caustic juice of the Manchioneel the result is said to be most beneficial.

The number of plants which are believed to be antidotes to snake-poison is very large. Poisonous snakes are widely distributed, and the injuries they inflict cause more deaths than possibly all the poisonous plants put together. It is not a matter of surprise therefore that in all ages efforts have been made to discover some antidote to snake-poison.

It is very remarkable that one genus of plants, the distribution of which is as wide almost as that of poisonous snakes, has been generally credited with the power of healing snake-bites. This is the genus *Aristolochia*. In many countries these plants are called Snake-roots. This name has been applied to them, not as is supposed in accordance with the so-called *doctrine of signatures*, from some fancied resemblance of the roots to snakes, but, according to Hanbury and Fluckiger, on account of the wide-spread application of the roots and other parts as antidotes to snake-bites.

The genus *Aristolochia* consists of about 180 species of plants widely distributed throughout tropical and temperate regions. They are inhabitants chiefly of tropical America, are rare in the North temperate zones, occasionally distributed in tropical Asia, and moderately frequent in the Mediterranean region.

They are herbs or shrubs often twining over trees. The flowers are remarkable for the peculiar inflated form of the calyx perianth, which is sometimes large, and of a lurid colour. The woody stem consists of radiating plates of wood surrounding a pith, and encircled by the bark. Hence there are no concentric rings as in the wood of dicotyledonous

plants generally. The wood, as indeed all parts of species of *Aristolochia*, possesses a strong smell. Most members of the genus contain in their root a volatile oil, a bitter resin, and an extractable acrid substance, which have rendered them celebrated in all times and countries as stimulants of the glandular organs and the functions of the skin.

Aristolochia is represented in England by *A. clematitis*, L., the common Birth-wort. It is a low growing shrub, with stalked heart-shaped leaves, in the axils of which the yellow trumpet-shaped flowers are produced in clusters.

The drug Serpentary is produced by a North American species, *A. Serpentaria*, L. This has superseded the use of the Aristolochias of Europe, which, besides *A. clematitis*, L., are *A. rotunda*, L., *A. longa*, L., *A. pallida*, Willd., and *A. sicula*, Tineo, all of which are chiefly found in the Mediterranean region.

In the West Indies, *A. grandiflora*, Vahl, has enormous flowers, and is believed to be poisonous. Other species, such as *A. odoratissima*, L., and *A. trilobata*, L., are reputed to possess valuable medicinal properties. About twenty species are distributed in Cuba and Hayti. More than forty species are natives of Mexico and Central America, and the head-quarters of the genus may be said to exist in tropical South America.

As already mentioned, the belief in the antidotal properties of species of *Aristolochia* is widely diffused over both hemispheres. Endlicher speaks of them as follows: 'Species .... efficaces, adversus serpentum morsus unanimi gentium praeconio celebrantur.' Theophrastus extols as a remedy for the bites of a snake a drink made by infusing in wine a Mediterranean species, *A. pallida*, Willd. Cicero, Pliny, Nicander, and many others have all recognised the universal belief in the efficacy of *Aristolochia* as an antidote to snake-poison. On the authority of Dr. Hance it is stated that the Arabs are accustomed to use the leaves of *A. sempervirens*, L., when bitten by poisonous snakes, and a similar remedy from *A. indica*, L., is in use in India.

The belief in the antidotal powers of *Aristolochia* is very prevalent in the New World, and especially in tropical America.

These plants are known to be powerful stimulants, and they are regarded by modern physicians as diaphoretics, stimulant tonics, and emmenagogues. Their antidotal properties are however not fully established. The array of testimony in favour of their alexiteric properties is nevertheless so overwhelming that it is incredible that these virtues should be purely imaginary, and the subject seems to demand a careful and dispassionate investigation[1].

The Virginian Snake-root, *A. Serpentaria*, was in great repute amongst the early Indian tribes as a cure for the bites of venomous snakes. It is chiefly used now as a simple stimulant tonic. It is stated by Barham[2], in respect to *A. odoratissima*, L., that 'the roots and seeds are very bitter, hot, and odoriferous, and are most excellent alexipharmics or counter-poisons, strengthening the heart, stomach, and brain; they cure the bites of serpents, and the poison of Indian arrows. I am of opinion, it exceeds the Spanish Contrajerva, especially in dropsies.'

The Spanish Contrajerva here mentioned refers to species of *Dorstenia*, of which *Dorstenia Contrajerva*, L., and *D. braziliensis*, L., have long been known as counter-poisons. In common with species of *Aristolochia*, these Dorstenias possess certain stimulant properties which doubtless brought them first into notice. An interesting account with plate is given of *Dorstenia Contrajerva*, by Descourtilz in Flore Medicale des Antilles, vol. iii. p. 256, t. 207. A good figure of *Dorstenia braziliensis* is given by Nees von Esenbeck in Plantes Medicinales, Dusseldorf, t. 99.

There is little more to be said respecting these plants, but it is interesting to note that the name of Contrayerva [or Contrayerba] applied to them is shared in Jamaica by a

[1] Dr. Hance has discussed this subject from the historical point of view in the Journal of Botany, vol. iii. (new series), p. 72, and some of the facts mentioned by him are here quoted.

[2] Hortus Americanus, p. 44.

species of *Aristolochia*, where indeed the term is restricted to *Aristolochia odoratissima*, L.

Under the name of Guaco more than one plant in Central and South America has been credited with the power of curing snake-bites. The name is commonly used in regard to a member of the Compositae, *Mikania Guaco*, H. B.; but here we have again a similar name applied, and the same powers ascribed to one or two local species of *Aristolochia*.

Mikania Guaco is a widely diffused climbing shrub, found in the West Indies and from Nicaragua to Brazil. It is figured by Descourtilz in Flore des Antilles, t. 197, and by Humboldt and Bonpland, Plantae Æquinoctiales, t. 105. It appears in Baker's Monograph of the Brazilian Compositae, under the name of *Mikania amara*, var. *Guaco*.

Mr. Robert B. White of La Salada, New Granada, in a communication to the Royal Gardens, Kew[1], gives his personal testimony in favour of *Mikania Guaco* as the true Guaco of tropical America. He states that 'there are two varieties, one with green stems, the other called "morado" with purple, the latter being the most prized.' There are several species of snakes in the country whose bite is deemed mortal, some of them killing in a very few hours, but Mr. White, who has lived in the Choco and other snake-infested regions many years, testifies that the Guaco, properly and promptly administered, is a cure for the bite of the most venomous.

The name Guaco was used to establish a new genus of Aristolochiae, and *Guaco mexicana*, Liebm. was a plant of this genus which had the highest reputation as an antidote for snake-bites. This genus has not however been recognised in the Genera Plantarum of Bentham and Hooker. In the Kew Museums there are specimens of two species of *Aristolochia* known in the Bay of Honduras as Guaco. One of these, described by Mr. G. W. Skinner as the more powerful, is also used by the natives bound round their legs when they

[1] Pharm. Journ. vol. xi. (3.) p. 369.

go into the bush to protect themselves from snakes. *A. panduriformis*, Jacq., is the Raiz de Mato of Venezuela; *A. fragrantissima*, Ruiz., is the celebrated Bejuco de la Estrella of Peru. Dr. Weddell was assured by the Bolivians in the province of Yungas that the crushed leaves of the Vejuco, *A. brasiliensis*, Mart., were an infallible cure for snake-bites. Señor Triana, the accomplished investigator of the flora of New Granada, found *A. tenera*, Pohl., in daily use in similar cases as a never-failing remedy under the name of Matos.

There are three species of *Aristolochia* in India which are in repute as antidotes for snake-bites. These are *A. indica*, L., *A. bracteata*, Retz., and *A. longa*, L. The first was known amongst the early Portuguese settlers as Raiz de Cobra, and is widely distributed over India. The local name amongst the natives is Sapsun. Mr. Lowther, Commissioner at Allahabad, carried out some interesting experiments with the leaves of *A. indica*, L., as an antidote for snake-poison. In his opinion they have proved an infallible remedy. In the experiments cited by him, but too long to be reproduced here, the leaves were bruised and applied to the wounds, and were also reduced to a pulp and given internally: three medium-sized leaves were usually bruised and mixed with an ounce of water[1].

Having thus passed in review various instances in which species of *Aristolochia* have been considered specifics in the treatment of snake-bites, it only remains to mention a few other plants to which this power has been attributed. The Snake-wood of the East Indies (*Strychnos colubrina*, L.) is in great repute as a remedy for the bites of snakes, as also in the treatment of skin-diseases. The Button Snake-root of North America is *Liatris squarrosa*, Willd., a perennial herb belonging to the Compositae. Its tuberous roots are considered a cure for the bite of the rattlesnake, and hence called Rattlesnake-master. A similar power is ascribed to the large knotted root-stalks of the Black Snake-root, *Cimicifuga racemosa*, Ell. The bitter and acrid root of *Cissampelos*

[1] Pharm. Journ. vol. xi. (3.) p. 411.

Pereira, L., is used in Martinique against the bite of the dreaded Fer-de-lance (*Trigonocephalus*). *Viola ovata*, Nutt., an American species, is a reputed specific against rattlesnake-bites. The roots of *Oxalis sensitiva*, L., are recommended for scorpion-bites, but appear to have no reputation for the bites of snakes. The singular embryo of *Ophiocaryon*, resembling a snake coiled up inside the nut, gives the name of snake-nut to the fruit; but here again the plant does not appear to be used as an antidote.

The Brazilians consider the leaves of *Casearia ulmifolia*, Vahl, a member of the Samydaceae, 'a certain remedy against the bites of the most venomous kinds of snakes.' The root of *Polygala Senega*, L., or the Senega Snake-root, an erect slender herbaceous plant, native of North America, is supposed by the Indians to resemble the tail of a rattlesnake and to be a cure for its bite. This same root is used in Europe on account of its stimulating action on the pulmonary mucous membrane. An allied species, *P. Serpentaria*, Eckl., has a reputation for curing snake-bites amongst the natives of South Africa. The Snake-root of Brazil, called Raiz de Cobra, appears to be *Chiococca anguifuga*, Mart. This possesses a musky smell similar to that of a snake which is said to have suggested its use as an antidote. The root of this plant is known as Caïnça, and is used in Europe as a diuretic and a purgative in cases of hydrophobia.

Again, *Ophiorrhiza Mingos*, L., known in the Malayan Islands as Earth-gall, a low bushy shrub, also a member of the Rubiaceae, with intensely bitter roots, is popularly reputed to be a cure for snake-bites. According to some writers, the sap of *Corypha umbraculifera*, L., and *C. sylvestris*, Willd., is an emetic, and is considered also an alexipharmic.

In 1883 Professor Macowan, of the Cape Botanic Garden, brought forward the possibility of utilizing *Leonotis Leonurus*, R. Br., as a medicinal plant. It was found on inquiry that this plant had a local reputation as a cure for snake-bites and possessed very powerful properties. It is smoked by the Hottentots, who call it Duyvel's tabak.

A decoction of the leaves and root of *Uvularia grandiflora*, Smith, is considered by the natives of North America a cure for the bite of the rattlesnake, and the fronds of *Botrychium virginianum*, Sw., are a reputed alexipharmic in St. Domingo.

It would appear from the foregoing enumeration of plants reputed to possess the property of counteracting the influence of snake-poison that the larger number of species belongs to the natural order Aristolochiae, and exclusively to the genus *Aristolochia*. Altogether twelve species of *Aristolochia* are here mentioned. Next in importance come two or more species of *Mikania* and one species of *Liatris* belonging to the natural order Compositae. Two species of *Dorstenia* belonging to the natural order Urticaceae are mentioned. Two species belonging to the genera *Chiococca* and *Ophiorrhiza* represent the natural order Rubiaceae. The following natural orders are each represented by one genus, viz., Ranunculaceae by *Cimicifuga*; Loganiaceae by *Strychnos*; Memispermaceae by *Cissampelos*; Violarieae by *Viola*; Geraniaceae by *Oxalis*; Polygaleae by *Polygala*; Liliaceae by *Uvularia*; Palmae by *Corypha*; and Filices by *Botrychium*.

It is only necessary to add that this enumeration of the plants reputed to possess alexipharmic properties is offered without any expression of opinion as regards their value. It is chiefly intended as an attempt to bring together for the first time a summary of information on the subject in order that inquiry may be made to confirm or refute the popular opinion respecting them. Opportunities to test the action of these plants on a person actually bitten by a well-known poisonous snake are seldom offered to a competent investigator. But as material is being brought together which can be carefully tested by chemical and therapeutical investigations, the most prominent of these plants, such as species of *Aristolochia* and *Mikania*, deserve very careful attention.

Notes on the Genus Taphrina.

BY

BENJAMIN L. ROBINSON.

DURING the winter of 1886–7 I had an opportunity to study, from dried and alcoholic material, a number of American and European species of the genus *Taphrina*. As the literature of the group, particularly on the American forms, is rather scanty, the notes which I have been able to make may be of assistance to those who wish to continue the study of this interesting group. In the systematic examination of European species much valuable aid has been derived from the papers of Sadebeck[1] and of Johanson[2]. These writers, it will be noticed, differ in the names they retain for the group; and a brief explanation of the synonymy of the genus will not be out of place.

The species, combined by Sadebeck, in 1883, into a single genus, were formerly classed in three closely related genera, *Taphrina*, Fries, *Ascomyces*, Mont. et Desm., and *Exoascus*, Fuckel. Of these genera the first is the oldest, having been described by Fries as early as 1815 under the name of *Taphria*, which, to avoid possible confusion with an insect genus, was in 1825 altered to *Taphrina*. In his paper just mentioned Sadebeck has preferred, although without stating his reasons, to retain for the combined genus the youngest of the three names, that of *Exoascus*, Fuckel. Johanson agrees with Sadebeck in thinking that all the species should be combined into a single genus, but, seemingly with much

[1] Untersuchungen über die Pilzgattung *Exoascus*, in Jahresbuch der wissenschaftlichen Anstalten, Hamburg, 1883, pp. 93–124.

[2] Om Svampslägtet *Taphrina*, in Ofversigt af Kongl. Vetenskaps-Akademiens Förhandlinger, 1885, Stockholm, N:o I, pp. 29–47.

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more regard for the rules of priority in nomenclature, retains the name *Taphrina* of Fries. There appears to be all the more reason for this from the fact that, as early as 1866, Tulasne[1] revised the genus of Fries and expanded its limits so that it might take in all the species then known of *Ascomyces* and *Exoascus*, thus using the name *Taphrina*, so far as the knowledge of the time enabled him, in the same sense as it is at present employed. From these considerations it seems best to follow Johanson in calling the group '*Taphrina*, Fries, char. a Tulasne emend.,' a sort of nomenclature which, if not brief, is yet in accord with priority, and incapable of being misunderstood.

The members of this genus are in structure among the simplest of the Ascomycetes, and in them no trace of sexual function has yet been found. They present also some features of similarity to the Saccharomycetes, to which group there seems a growing tendency to consider them closely related[2]. With one possible exception, all the species known are parasitic in their habit. They seldom attack herbs, but are commonly found on shrubs or trees, especially those of the Rosaceae, whence the chief economic importance of their study. Their mycelia penetrate the tissues of the host to various depths where, in some species at least, they pass the winter. In the spring they begin their development anew, and enter the young shoots and leafy parts of the plant attacked; here they spread their hyphae beneath the cuticle, or in some species just below the epidermis, forming a branching network. From this sort of hymenium the asci arise. They are more or less cylindrical in form, and usually occur in great numbers, densely packed together. They are found between the cuticle and epidermis, being developed in the species which have their hymenia beneath the epidermis, as enlarged ends of vertical threads which,

[1] Super Friesians Taphrinarum Genere, in Ann. des Sciences nat., sér. 5, Tome v, 1866, p. 122.

[2] See De Bary, Vergl. Morph. und Biol. der Pilze, Mycetozoen und Bacterien, Leipzig, 1884, pp. 286–294.

arising from the subepidermal network, make their way between the cells of the epidermis and become developed into asci which, as in the other species, are formed between the cuticle and epidermis. In several species each ascus is borne on a specialized portion of the mycelium known as the stalk-cell. These cells vary considerably in form, being sometimes long and slender, cylindrical or obconical, or, on the other hand, short and broad with flat and truncate bases. Within each ascus generally eight nearly spherical spores are formed, but the octosporic condition is often not permanent, for while yet in the ascus the spores divide by a process closely resembling the budding of the Saccharomycetes. In this way the asci frequently become filled with very numerous reproductive bodies, sometimes resembling the eight original spores, except in their smaller size and rather more oblong or oval form, in other cases becoming very minute and bacteria-like. The asci of several species are always polysporic at maturity, and no eight-spored condition is readily discernible in their development. Even in them, however, there seems reason to believe that the many-spored form is secondary, resulting from spore-division. As the asci grow they raise up the cuticle from the epidermis, and at some period, early in some cases, near maturity in others, break through to the surface. The release of the spores when the asci have not been subjected to any violent rupture, to which their delicate structure and superficial position render them liable, seems to be effected through a rather small orifice at the summit of the ascus.

The presence of a *Taphrina* is manifested by the host in one or more of several ways: namely, by the occurrence on the leaves of roundish or irregular blotches, varying in colour from yellow to purple according to the species of the parasite; by a curling or crisping of the leaves, sometimes accompanied by a toughening or cartilaginous modification of the leaf-texture; by the swelling out of the softer parts of the leaves between the nerves, rendering the surface convex on one side and concave on the other; by deformity

of the fruit; and, lastly, by the swelling and distortion of the twigs and young branches.

In showing in some degree the affinities within the group, as well as in furnishing a means of ready determination of the individual species here described, the following synopsis of the American species which I have been able to examine may be found useful. Tulasne, in subdividing his new genus, *Taphrina*, had regard to the lines of division between the older genera of which it was composed, and accordingly grouped his species into those with so-called polysporic asci (*Taphrina*, Fries, and *Ascomyces*, Mont. et Desm.), and those with eight-spored asci (*Exoascus*, Fuckel). But, as just stated, the polysporic condition is probably secondary, and the spores of all the so-called octosporic species are very liable to multiply within the ascus. This distinction therefore does not seem of primary importance, and in arranging the American species it is better to follow Sadebeck and Johanson in grouping the species according to the depth to which their mycelia penetrate the tissues of the host-plant. It will be understood that the following synopsis is not intended to be exhaustive, as there are several forms of *Taphrina* more or less perfectly known in America which I have been unable to examine.

Synopsis of American Species examined.

I. Mycelium penetrating intercellularly the inner tissues of the host.

(1) Fertile portion of the mycelium between the epidermis and the cuticle,

(*a*) Asci raised on stalk-cells,

T. Pruni (Fuckel), Tul.

T. deformans (Berk.), Tul.

(*b*) Asci without stalk-cells,

T. purpurascens (Ellis et Evh.).

(2) Fertile portion of the mycelium beneath the epidermis,

T. Potentillae (Farw.), Johans.

T. flava, Farw.

II. Mycelium spreading itself just below the cuticle, and not entering the tissues of the host.

(*a*) Asci with stalk-cells,

T. alnitorqua, Tul.

(*b*) Asci without stalk-cells,

T. aurea (Pers.), Fries.

T. caerulescens (Mont. et Desm.), Tul.

For *Exoascus Wiesneri*, Rathay, and *Ascomyces Quercus*, Cooke, see *Taphrina deformans* and *T. caerulescens* respectively.

T. PRUNI (Fuckel), Tul.

Exoascus Pruni, Fuckel, Ennumeratio Fungorum Nassoviae, p. 29.

This species occurs frequently in the United States upon *Prunus domestica*, L., and causes a peculiar hollow deformity of the fruit, the so-called 'plum-pocket' (Narren-Taschen). Late in June the infected plums reach almost their mature size, but consist merely of a thin shell having instead of pulp and stone only a few threads stretched irregularly across the cavity within. A *Taphrina*, probably identical with this, attacks several of our native species of *Prunus*, and has been found on *P. maritima*, Wang., Dartmouth, Mass., on *P. virginiana*, L., near Lake Willoughby, Vt., and on *P. serotina*, Ehr., Cambridge, Mass. On the last-mentioned host the fruit, which is normally nearly spherical, when infected becomes elongated or even somewhat spindle-shaped, and early attains a size several times greater than at normal maturity. The stamens and floral envelopes also suffer hypertrophy and remain attached to the base of the fruit in an involucre-like mass.

The asci are formed in very great numbers; early in their development they break through and almost obliterate the cuticle, and form a dense and continuous layer over the whole surface of the fruit, which later becomes hoary from the escaping spores. In general form the asci are long and slender, cylindrical, truncated or rounded at the summit,

and slightly tapering below. On *P. domestica* nearly all the asci examined have been more slender in proportion to their length than those described by Sadebeck. Furthermore there appears to be a sort of dimorphism among them, such as Johanson describes in the asci of *T. alnitorqua*; for, beside the long and very slender ones, which are usually octosporic at maturity, there are others, more often polysporic, which are considerably shorter and thicker. In length the slender asci vary from 43 μ to 60 μ and in thickness from 5½ μ to 7 μ, while the asci of the stouter kind are 27–35 μ in length and 9–12 μ in thickness. The stalk-cells are 12–18 μ long and 5–8 μ thick; they rest upon the epidermis, but do not intrude between the cells. The nearly spherical spores are normally eight with a diameter of 3–4½ μ, but become much more numerous and smaller by division.

T. DEFORMANS (Berk.), Tul.

Ascomyces deformans, Berk., Outlines of British Fungology, p. 376.

Ascosporium deformans, Berk., ibid., in description of plate I.

Exoascus deformans, Fuckel, Ennumeratio Fungorum Nassoviae.

Exoascus Wiesneri, Rathay, in Oesterreichische Botanische Zeitschrift, Jahrgang xxx, No. 7, p. 225.

The ordinary form of this species occurs upon peach-trees, and causes the crisping and wrinkling of the leaves known as the 'peach-curl.' On infection by the parasite, the leaves not only are distorted but become much thickened and take on a sort of cartilaginous structure. The asci are borne on both sides of the leaf, but in greater numbers upon the lower surface. Although the material which I examined was shown by the perfection of the spores to be mature, the asci were considerably shorter than those described by Sadebeck. The measurements were as follows: length of asci 26–32 μ, thickness 6–10 μ; height of stalk-cell 9–12 μ, mean thickness 3½–4½ μ, thickness at base often as low as 2 μ. The spores,

when eight in number, are nearly spherical and $3\frac{1}{2}$–$5\frac{1}{2}$ μ in diameter, but by division their size is reduced to about 2 μ.

Beside this form on the peach, a *Taphrina* has been found at Germantown, Pa. (Mr. Mehan), on the leaves of 'escaped cherry-trees.' As to the species or variety of the host, I regret to say, I can give no exact information. The parasite is probably the *Exoascus Wiesneri* of Rathay, which is now regarded merely as a form of *T. deformans*. As in the peach-curl, the infected cherry-leaves become much wrinkled and distorted; the small branches attacked are also somewhat modified and show a tendency toward forming 'witches' brooms' (Hexenbesen), such as are described by Rathay[1]. The asci are developed on both surfaces of the leaf, and closely resemble those of the typical form on the peach, though perhaps a little more slender; in length they are 27–33 μ, in thickness 5–8 μ. The stalk-cells are taller than any I have seen on peach-leaves, and do not taper so much below; they are 17–18 μ high, and 5–7 μ thick.

A *Taphrina*, probably the same as this, has been found several times in Massachusetts deforming the leaves and branchlets of *P. serotina*, Ehr.

T. PURPURASCENS, sp. nov.

Ascomyces deformans, var. *purpurascens*, Ellis et Everhart, North American Fungi.

This form occurs on the leaves of *Rhus copallina*, L., and has been found in Massachusetts at Dartmouth, Salem, Wood's Holl, and other localities; in Connecticut at New London; and also in New Jersey. The infected leaflets may be recognized by their dark purple colour and wrinkled appearance, as well as by their limp and pendent condition. Furthermore, it may be noted that the softer parts of the leaf tissue swell out between the nerves and become convex above and concave beneath. The dark colour is at first

[1] Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Math. und Naturwiss. Kl., Wien, Band lxxxiii (1881), p. 267.

confined to roundish blotches, but these soon become irregularly confluent and cover much or all of the surface of the leaflet. Microscopically, the most noticeable modification in the infected parts of the leaf is the very compact and palisade-like structure which the spongy parenchyma and epidermis assume.

The asci are formed on both sides of the leaf, and reach maturity late in June or early in July. They are 24–32 μ long, and somewhat dumb-bell shaped in outline, being constricted in the middle apparently by the cuticle of the host; the thickness of the exserted portion is 9–14 μ, of the constricted part 6–11 μ, and of the broad base 9–21 μ. In size and shape the asci closely resemble those of the European *Exoascus Carpini*, Rostrup; from that species however this form on *Rhus* is well distinguished by the presence of a mycelium which penetrates the inner tissues of the host-leaf. From *T. deformans*, of which it was once classed as a variety, *T. purpurascens* differs not only in the size and form of its asci but in having no stalk-cells. The spores are eight in number and ellipsoidal in form; their maximum diameter is 3½–5 μ and minimum 2½–4 μ. Like the spores of other species they are very liable to division while still in the ascus.

The first notice of this form is in 'Notes on the Third and Eleventh Centuries of Ellis's North American Fungi'[1] by Dr. Farlow, who gave a partial description of specimens found at Dartmouth, Mass., by Dr. B. D. Halsted. It as there considered as possibly a variety of *Exoascus deformans* or, at least, a related species. Mention was made of a similar form on an African *Rhus* described by Magnus, as the writer believed, although he could not at the time recollect where it was published. I have since been informed by Dr. Farlow that he was in error, and that the description which he had in mind was by Dr. F. Thomas instead of Magnus. In the article, published in 1883[2], Thomas describes a deformation of

[1] Proceedings of the Amer. Acad., vol. xviii (1883), p. 85.
[2] Berichte der Deutschen botanische Gesellschaft, Bd. i (1883), Berlin.

some leaves of *Rhus pyroides*, Burch., from South Africa, which he ascribed to the presence of a parasitic fungus. He states, however, that from his dried material he could only make out several minute processes, on the surface of the leaf, resembling the basidia of an *Exobasidium*. It seems not improbable that this form, on further investigation, may prove the same as our American species, especially as in his description of the changes in the infected leaves, Thomas speaks of a dense and palisade-like structure taken on by the spongy parenchyma.

T. POTENTILLAE (Farw.), Johanson.

Exoascus deformans, var. *Potentilla*, Farw., in Proceedings of Amer. Acad. vol. xviii (1883), p. 84.

This distinct and well-marked species has been frequently found in various places in Massachusetts and Connecticut. Early in June it causes, on the leaves of *Potentilla canadensis*, L., little, roundish, yellow spots, which become convex above and concave beneath, and soon deepen in colour from yellow to brown and then to purple. Johanson, in describing the deformities produced by this species on *P. Tormentilla*, Scop., speaks of the swelling of the petioles and curling of the leaves; but although I have looked over a number of dried and a few fresh specimens of *P. canadensis*, attacked by the parasite, I have not succeeded in finding any deformity in the petioles or stems.

The peculiarities of the mycelium in this and the succeeding species have been noted already in the synopsis. The subepidermal position of the fertile threads naturally influences the form of the ascus so that the upper part only becomes expanded and contains the spores, while the lower portion is merely a very slender pedicel which, passing between the cells of the epidermis, connects the ascus with the mycelium below. In *T. Potentillae* the asci, which are borne on both sides of the leaf, are club-shaped and very slender. The spore-bearing portion is 25–33 μ long and 8–10 μ thick, while the slender pedicels, which are usually longer on the upper

than on the under surface of the leaf, vary from 20–30 μ in length, and are often less than 2 μ thick. The spores are eight or many, 3–4 μ in diameter.

T. FLAVA, Farw., in Proceedings of Amer. Acad. vol. xviii (1883), p. 84.

Exoascus flavus, Farw., Ellis' N. A. Fungi (1879), No. 300.

This species must be carefully distinguished from the more recent and very different *Exoascus flavus* of Sadebeck, which Johanson, with deference to the priority of Dr. Farlow's name, has called *Taphrina Sadebeckii*. *T. flava*, Farw., is also quite distinct from *Exoascus Betulae*, Fuckel, which also occurs in roundish spots on the leaves of various species of *Betula*, but has not, to my knowledge, been found in America. If it does occur here it may be distinguished from *T. flava* by its shorter and more slender asci, its well-developed stalk-cells, and the absence of any subepidermal mycelium.

T. flava, Farw., has been found most often on *Betula alba*, var. *populifolia*, Spach., in Eastern Massachusetts and New Hampshire, but has also been collected on Mt. Washington, N. H. (E. Faxon), on *B. papyracea*, Ait. It appears on the leaves of either host in June as bright yellow, circular spots, which vary considerably in diameter. In some dried material examined these spots were distinctly concave above and convex beneath. The asci are very numerous and densely packed together on both sides of the leaf. In outline they are rectangular, being truncated at each end; their length is 31–52 μ, and thickness 17–26 μ. Within each ascus there is a great number of very small oblong spores. The asci have no proper stalk-cells, but in a thin section the subepidermal mycelium (hymenium) is seen to be connected with the asci by very slender pedicels which pass vertically upward between the cells of the epidermis and expand abruptly into the asci above. When the upper portion only of such a pedicel is seen, it may appear like a downwardly directed process

from the ascus, resembling, except in its more slender form, one of the rootlike appendages which are really developed downward from the asci of *T. aurea* and *T. caerulescens*; but its different nature becomes clear when its connection can be traced with the mycelium below. From the position of its mycelium and the mode of forming its asci, it is evident that this species is closely related to *T. Potentillae*, just described, however dissimilar it may seem in the size and shape of the asci themselves and the spores they contain.

T. ALNITORQUA, Tul., in Ann. des Sciences Nat., sér. 5, Tome v. p. 130.

Ascomyces Tosquinetii, Westendorp, in Bull. de l'Académie royale de Belgique des sciences, sér. 2, Tome xi. p. 655.

Exoascua Alni, De Bary.

Exoascus alnitorquus, Sadebeck, Untersuchungen über die Pilzgattung *Exoascus*, p. 115.

This species is common in Massachusetts on the bracts of the fertile catkins of the alder. It develops a month or two earlier than the other *Taphrinae*, and, although easy to find, it is for some reason seldom in good condition for microscopic study. The bracts which are attacked grow abnormally long and thick, are variously curled and twisted, and become hoary with the escaping spores. The asci are borne on all parts of the infected bracts; they are 29–37 μ long and 6–10 μ thick. Although, as these measurements show, there is considerable variation in the length and thickness of the asci, I fail to find here the dimorphism mentioned by Johanson in the asci of this species in Sweden. Each ascus is furnished with a cylindrical stalk-cell 15–17 μ high and 6–8 μ thick. The spores are usually eight, sometimes many, spheroidal in form, and $3\frac{1}{2}$–6 μ in diameter.

In Europe *T. alnitorqua* has a form which occurs on the leaves of the alder, and, although not yet found in America, this form may well be looked for, as it is not improbable that it occurs here also.

T. AUREA (Pers.), Fries.

Erineum aureum, Persoon, Synop. Method. Fungorum, p. 700.

Taphrina populina, Fries.

Exoascus Populi, Thümen, in Hedwigia, Band xiii. p. 98.

Exoascus aureus, Sadebeck, Untersuchungen über die Pilzgattung *Exoascus*.

The only form of this species yet found in America attacks the fertile catkins of poplar trees. It is of frequent occurrence, and has often been collected on *Populus grandidentata*, Michx., in Massachusetts, at Springfield, Newton, and elsewhere. In the infected catkins several of the ovaries grow abnormally large, and, late in April or early in May, when the fungus reaches its fruiting stage, become golden-yellow from the orange-coloured asci of the parasite. The mycelium is only subcuticular, and does not enter the inner tissues of the host; each ascus, however, sends down an irregular rootlike process 20–40 μ long, which, making its way between the cells of the epidermis, even enters a little distance the hypoderm below. The entire length of the ascus, the process included, is 80–114 μ, and the thickness 16–19 μ. These measurements do not differ very much from those of Sadebeck, but Johanson, in describing the Swedish form which occurs on the leaves of *P. nigra*, L., gives the total length of ascus as only 47–49 μ. The spores are very numerous and of minute size.

T. CAERULESCENS (Mont. et Desm.), Tul., in Ann. des Sciences Nat., sér. 5, Tome v.

Ascomyces caerulescens, Mont. et Desm., Ann. des Sciences, sér. 3, Tome x. p. 146.

Exoascus caerulescens, Sadebeck, Untersuchungen über die Pilzgattung *Exoascus*.

Ascomyces Quercus, Cooke, in Ravenel's Fungi Amer. No. 72.

This is one of the most common and wide-spread species of the genus. It occurs on a number of our American oaks,

having been found on *Quercus alba*, L., and *Q. tinctoria*, Bart., at New London, Conn. (Dr. Farlow); on *Q. coccinea*, Wang., at Stoughton, Wis. (Prof. Trelease); on *Q. rubra*, L., at Bald Cap Mt. (3000 ft.), N. H., also at Ithaca, N. Y. (Prof. Trelease); on *Q. aquatica*, Catesby, and *Q. laurifolia*, Michx., at Green Cove Spring, Fla. (the late Dr. Geo. Martin); and on *Q. cinerea*, Michx., at Aiken, S. C. (Ravenel's Fung. Amer. No. 72). The fungus appears on the leaves of its host during June in roundish spots, which vary in size, and are grey or somewhat bluish in colour. On the leaves of *Q. rubra*, which I have examined, these spots were pretty definite in outline, and only 2–5 mm. in diameter; on *Q. tinctoria*, on the other hand, they were 10–12 mm. in diameter, and irregular in shape. The habit of the asci in regard to the side of the leaf upon which they are developed does not seem to be uniform on the different hosts. In his original description of *Ascomyces caerulescens*, cited above, Desmazière speaks of the asci as 'hypophyllus,' and that undoubtedly is their usual position, but upon the leaves of *Q. tinctoria* I have found them only on the upper surface. In general form the asci somewhat resemble those of *T. aurea*, but their rootlike processes are generally shorter and penetrate the interstices of the epidermis to a less depth than in that species. The asci may furthermore have two or even three of these processes, which, in that case, are apt to be short and blunt. In length the asci are 55–78 μ, and in thickness 18–24 μ. The spores, like those of the preceding species, are very numerous, minute, and bacteria-like.

By the kindness of Dr. Farlow I have had an opportunity to examine some of the original material of *Ascomyces Quercus*, Cooke, which was distributed as No. 72 in Ravenel's Fungi Americani. This parasite, which occurs on the leaves of *Q. cinerea*, corresponds perfectly, so far as I can see, with *T. caerulescens*, not only in the extent and shape of the spots in which it occurs, but in the size and form of the asci, which in both forms are polysporic. The only difference that I could find was in the size and shape of the spores. In *Ascomyces Quercus* they are oval in form, and vary in size from 4 μ

down to 1 μ and less, while in *Taphrina caerulescens* they are oblong or cylindrical, and usually less than 2 μ in diameter. As the size of the spores in these polysporic asci depends upon the extent of the subdivision of the original eight spores, a process which is very probably influenced by external circumstances, the diameter of such polyspores, so variable in the same species, can hardly be considered a character of sufficient definiteness to warrant the separation of forms which differ in no other particular.

In closing I wish to express my sincere thanks to Dr. W. G. Farlow, who very kindly furnished me with the material for studying this group, and aided my work with many valuable suggestions.

CAMBRIDGE, MASS., U. S. A.

NOTES.

APOSPORY IN THE CHARACEAE.—In his recent paper 'On Apospory and Allied Phenomena'[1] Prof. Bower criticises the view expressed by me in a paper on 'The Pro-embryo of Chara[2],' that the 'pro-embryo' of the Characeae represents the asexual generation in the life-history of these plants, and is in fact an aposporous sporophyte.

I fail to perceive that Prof. Bower's criticism touches the real merits of the case. My view does not necessarily lead to the conclusion that every lateral bud is to be regarded as an independent generation, nor to the assumption that the protonema of Mosses represents a third generation in the life-history of those plants, as Prof. Bower suggests. My argument is based, not upon any special virtue of 'laterality' of budding, but upon the general law that, in plants which present an alternation of generations, that which proceeds from the oospore is the sporophyte. If this holds good in Mosses, Ferns, etc., why should it not apply in the Characeae, where the oospore does not, as in the Fucaceae, give rise to a normal oophyte, but to something different? The idea of an aposporous sporophyte, though somewhat hazardous at the time my paper was written, has been fully justified by Prof. Bower's own researches.

My views on the subject have, however, undergone considerable modification, and I am glad to have this opportunity of stating that such is the case. But this is due, not to any *a priori* objections, but to facts which have come to light in recent years. I have always been conscious that the true significance of the pro-embryo of the Characeae would be made clear, not directly by the discovery of an asexual production of spores by the pro-embryo, but by the investigation of the embryology of other Algae, especially of the Florideae and the Phaeosporeae. This has been to some extent realised by Sirodot's remarkable observations on certain families of the Florideae, the

[1] Trans. Linn. Soc., vol. ii, Part 14.
[2] Journal of Botany, 1878.

Lemaneaceae[1], and the Batrachospermeae[2]. He finds that, in the Lemaneaceae, the carpospore gives rise to a creeping filamentous or flattened body which produces neither sexual nor asexual reproductive organs, but gives rise to erect lateral branches which eventually become independent and constitute sexual plants (oophytes). This case is comparable with that of the Characeae. In *Batrachospermum*, the carpospore likewise gives rise to a filamentous body, the Chantransia-form, from which the sexual Batrachospermum-plant eventually springs as a lateral branch. This case, again, is so far comparable with that of the Characeae. But there is this peculiarity, that the Chantransia-form of *Batrachospermum* produces spores. This would seem to confirm my view concerning the nature of the pro-embryo of the Characeae, but, as a matter of fact, it does not. These Chantransia-spores are of the nature of gonidia; that is, they simply reproduce and multiply the Chantransia-form; they do not give rise to Batrachospermum-plants. Hence, they do not prove that the Chantransia-form is the sporophyte in the life-history of *Batrachospermum*; nor does their presence absolutely disprove that the Chantransia-form is the sporophyte, though it renders it improbable. The Chantransia-form is probably analogous to the protonema of Mosses; it is the pro-embryo of the oophyte, just as the protonema is the pro-embryo of the oophyte, though the one is developed from a sexually-produced, the other from an asexually-produced, spore. If this be so, then the analogy holds good also in the case of the Lemaneaceae and of the Characeae. The development of the pro-embryo in these plants is then indicative, not of an alternation of generations, but simply of indirect or heteroblastic development.

S. H. VINES, Cambridge.

METHOD FOR PRESERVING THE COLOURS OF FLOWERS IN DRIED SPECIMENS.—The preservation of the colour in dried flowers, leaves, and stems is a matter which has interest for a considerable section of the public, and as a method, not generally known in Britain, by which this is secured has been practised in Berlin with great success for several years, I propose to give a description of it. It is described by Mr. Hennings in the Abhandlungen des botanischen Vereins des Provinz Brandenburg, Bd. xvii (1885).

[1] Ann. d. sci. nat. sér. 5, Tom. xvi.
[2] Les Batrachospermes, 1884.

The flowers to be preserved are put into water saturated with sulphurous acid, to which methylated alcohol (ordinary strength) is added in the proportion of one part of alcohol to three parts of water. Plants with thick leaves are left in the fluid for a day or a day and a half, delicate flowers only from five minutes to half an hour. The specimens are then removed and the fluid on the surface is allowed to evaporate by exposure to the sun or artificial heat, and when this has taken place the specimens are then placed between sheets of drying paper in the usual way. As a rule it is not necessary to change the paper. Treated in this way plants either retain from the first their natural colour, or, as sometimes happens, the colour, which alters slightly at first or even disappears altogether, is regained in a short time. Flowers especially scarcely lose any of their natural splendour. A difficult part of the process in the case of delicate flowers is the laying out of the parts upon the drying paper after treatment in the solution.

Not only does the method preserve colour but it also hastens the process of drying. As instances of this Mr. Hennings mentions that the globose stems of *Euphorbia globosa* were dried in three days, the juicy and thick rosettes of species of *Echeveria*, *Crassula*, and *Sempervivum* in two days, the fleshy inflorescences of Orchideae, Araceae, Melastomaceae in one day, and all kept their natural colour completely, or nearly so. Plants too which usually turn black on drying, such as *Lathraea squamaria*, *Melampyrum*, and others, when treated in this way keep their natural colour.

A solution once made may be used over and over again.

SELMAR SCHÖNLAND, Oxford.

THE APICAL MERISTEM IN THE ROOTS OF PONTEDERIACEAE.—The structure of the roots of the Pontederiaceae has already been repeatedly investigated. Nägeli[1], who first gave an account of them, chiefly directed his attention to the mode in which the rootlets of the adventitious roots in *Pontederia* (now *Eichhornia*) *crassipes*, Mart., arose. As far as the first stages of their development are concerned I have nothing to add to his observations. As to more advanced stages I cannot agree with him, but I shall refer to this again later on.

[1] Nägeli u. Leitgeb, Beiträge zur wissenschaftl. Botanik, Hft. 4 (1868), p. 138.

Treub[1], in his elaborate paper on the apical meristem of the roots of monocotyledonous plants, tried to make out the apical meristem of the main roots themselves. According to him these have distinct initials for the plerome, common initials two layers thick for the periblem, dermatogen, and the calyptra, but at the same time he found that in the calyptra further divisions take place by means of which it acquires a certain amount of independence. He ascribed this structure also to Iridaceae, *Sparganium*, *Butomus*, and doubtfully to *Alisma*.

The next who took up the same subject was Flahault[2]. He examined the adventitious roots[3] of *Eichhornia crassipes* and the primary roots of *Pontederia cordata*, L. The primary roots of *P. cordata* have, according to him, distinct initials for the plerome, two or three common initials (on longitudinal section) for the periblem and dermatogen, and distinct initials for the calyptra. In studying the structure of the apical meristem of the adventitious roots of *Eichhornia crassipes*, he came to the conclusion that the characters of the apex of these roots are not absolutely fixed, and that the initials of the different tissues may become more or less specialised. But he shows that he is not quite certain about this point by adding that the epidermis may *very likely* be independent of the cortex even at the apex of the root, though he never observed this fact in the embryo of *Pontederia cordata*, and he concludes by saying that the epidermis, when once differentiated, does not take any part in the formation of the rootcap.

Flahault says that he hesitated a long time before he came to the above-mentioned conclusions. Perhaps he would not have done so if he had not used the same method in preparing his sections as Treub —boiling in a solution of calcium chloride till nearly all the water was evaporated. I think that this method is too severe for tissues so delicate as the apices of roots of water-plants. Much better results may be obtained by soaking the sections in potash for twenty-four hours, treating them with acetic acid and then mounting in glycerine. Sometimes I have examined sections in glycerine directly after they were cut, in other cases I stained them with Kleinenberg's haematoxylin after treatment with potash, and mounted them in canada balsam. I found, like Flahault, that the characters of the apex of the adventitious roots

[1] Le méristème primitif de la racine dans les monocotylédones, Leiden, 1876.

[2] Ann. des sciences nat. sér. 6, vol. vi. pp. 1–168 (Pontederiaceae, p. 50).

[3] Though he does not state distinctly that he used the adventitious roots for this investigation, this must be concluded from his remarks.

of the Pontederiaceae are not fixed, and the object of this note is to show the connection between the different appearances which they may exhibit in longitudinal section.

If transverse sections are made through a node of *Eichhornia azurea*, Kunth, or *E. crassipes*, Mart., on which adventitious roots are not yet visible, one is pretty sure to get some longitudinal sections of young roots still enclosed in the tissue of the stem. They do not come out from the stem quite horizontally, but as a rule there are a few of them cut nearly in a median plane in their apical portion. These show, when treated in the above-mentioned ways, that even in the youngest stages it is quite impossible to refer the rootcap to the same initials which give rise to the dermatogen and periblem. There is a distinct calyptrogen layer (Fig. 4, *c*) dividing by periclinal, rarely by anticlinal, walls. Other periclinal walls are not formed in the calyptra, but here and there anticlinal walls may be formed in other layers. Between the calyptrogen and the plerome there is only one layer of cells, giving rise to both dermatogen and periblem (Fig. 4, *i*), and besides there are distinct initials for the plerome. In short, the young adventitious roots of the Pontederiaceae have very much the same structure as the primary roots of *Pontederia cordata*, and belong therefore to the type of the Gramineae.

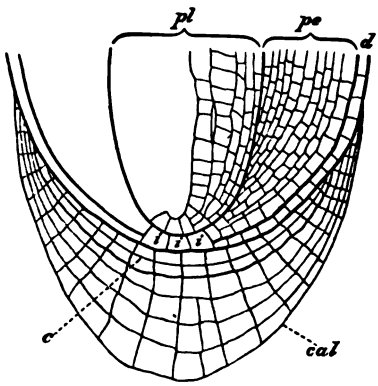

Fig. 4. *Eichhornia azurea*, Kunth.—Median longitudinal section of the apex of an adventitious root while still enclosed in the tissue of the stem: *pl* plerome; *pe* periblem; *d* dermatogen; *cal* calyptra; *c* cells of the calyptrogen; *i* initials of the dermatogen and periblem.

The number of cells forming the initial layer of the periblem and dermatogen varies from two to four (in longitudinal section) in the roots at the stage I have described, but if roots are examined when they have just broken through the tissue of the stem, the number of cells is fewer, often only one cell being seen undivided. At a further stage of development the dermatogen becomes quite independent, and extends

right round the apex, and thus two layers of cells are now seen between the calyptra and plerome (Fig. 5). I am not able to state at what age this final differentiation is effected; it seems to me to vary according to the conditions under which the roots grow, though I cannot exactly say what these conditions are.

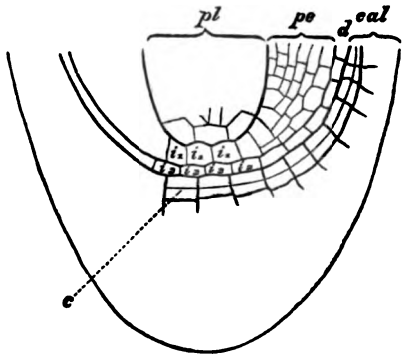

Fig. 5. *Eichhornia azurea*, Kunth.—Median longitudinal section of the apex of an old adventitious root: *pl* plerome; *pe* periblem; *d* dermatogen; *cal* calyptra; *c* calyptrogen; i_1 initials of the periblem (the cell to the right of the three lettered cells is also an initial); i_2 initials of the dermatogen.

As the roots have thus acquired the apical structure of *Pistia* and *Hydrocharis*, it might be supposed that their final differentiation is due to the disappearance of the calyptrogen layer, or rather to its inactivity, as happens in those genera; but this is not the case. Sometimes the rootcap dies off completely, and then it is quickly followed by the other parts of the apex, but usually the calyptrogen seems to be active as long as the apex is growing, though the rootcap, which grows very slowly, can be easily detached even in comparatively young roots. It certainly cannot be accidental that all the plants in which the most differentiated apical meristem of the roots has been found are monocotyledonous water-plants, and it may be noted that Holle[1] has found in *Vallisneria* a transition from the type of the Gramineae into the type of *Hydrocharis* and *Pistia*, just as I have observed it in *Eichhornia crassipes* and *E. azurea*.

I have still to add that the apical meristem of the rootlets in fairly advanced stages corresponds, as far as I have observed, with the type of the Gramineae, and Nägeli and Leitgeb's figure 5 cannot therefore represent a median section and satisfactorily illustrate the structure of a rootlet.

SELMAR SCHÖNLAND, Oxford.

[1] Bot. Zeitung, 1877, p. 542.

PRELIMINARY NOTE ON THE FORMATION OF GEMMAE ON TRICHOMANES ALATUM.—The plant on which the observations now to be described were made belongs to the Edinburgh Botanic Garden. Through the kindness of Prof. Dickson, who had already noted a similar peculiarity in a species of *Trichomanes* in a private collection in Edinburgh, the plant was placed at my disposal for detailed observation and culture. As noted by Prof. Goebel in a recent work dealing with the germination of certain Ferns, and especially the Hymenophyllaceae[1], the growth of the prothalli of this family is exceedingly slow, and, on this as well as on other grounds, I think it advisable not to delay the publication of facts already acquired till the close of the observations of cultures which are likely to extend over many months.

The plant of *Trichomanes alatum*, on which these observations were made, is in a strong, healthy condition, and on the upper and larger leaves there are numerous sori, bearing apparently normal and mature spores. It is on the lower leaves that peculiarities of development are to be seen; outgrowths of two kinds are formed at or near to the tips of the pinnae, and it is especially to be noted that they are actually vegetative outgrowths, as was shown to be the case in those aposporous Ferns which I have described elsewhere[2]. The outgrowths of the first type appear as ribbon-like prolongations of the laciniae of the frond, and several such may be found on a single leaf: they are only one layer in thickness, and may consist of two to four or more rows of thin-walled cells having the usual characteristics of a prothallus: they differ from the normal frond in the entire absence of those stiff hairs which are so numerous in this species. On the ends of these processes are borne numerous *sterigmata* [this term is adopted in the sense of Goebel, l. c. p. 82], many of which bear spindle-shaped *gemmae* similar in aspect and position to those described by Cramer[3]. Others may bear similar gemmae in various stages of development, while others again show merely a brownish point, where the mature gemma has broken away from its support. The results of cultivation of gemmae after removal from the sterigmata are as yet very incomplete, but I am in a position to state that germination does at least take place.

The outgrowths of the second type may start from any single marginal cell of one of the lower leaves of the plant: this grows

[1] Ann. Jard. Bot. Buitenzorg, vol. vii. [2] Trans. Linn. Soc. vol. ii. Part 14.
[3] Denkschr. der Schweiz. Nat. Ges. xxviii.

out into a long protonema-like filament, with transverse septa, and numerous lateral rhizoid processes: the cells contain chlorophyll, and the whole resembles moss-protonema, though the filaments are coarser. Ultimately the filaments widen out into flat expansions of ribbon-like form, and may bear gemmae as above described: again, single marginal cells of these ribbon-like expansions may grow out as protonemal filaments similar to those produced from the parent frond. No antheridia or archegonia have as yet been observed on any of the outgrowths above described.

We have here to deal with a very peculiar development, differing, I believe, from any hitherto described among the Hymenophyllaceae. In the first place it is to be noted that the gemmae correspond in structure and position to those described by Cramer: he ascribed those observed by him to one of the Hymenophyllaceae, a view which is supported by the recent observations of Goebel (l. c.). We now see in the Edinburgh plant the confirmation of this view, by the production of closely similar gemmae actually in connection with a specimen of *Trichomanes alatum*. But whereas Cramer's gemmae were borne on a prothallus bearing sexual organs, those of the Edinburgh plant are produced on processes resulting from a direct outgrowth from the fern-plant. How then are we to view these processes? Are they prothalli produced in an aposporous manner? Notwithstanding the failure as yet to note sexual organs on these outgrowths, I am inclined to the opinion that this is actually the case: that in the Edinburgh plant we have a fresh example of apospory, associated with a formation of gemmae, which, according to Goebel's observations, is not an uncommon mode of reproduction of the prothalli of Ferns. It will remain for detailed observation of the cultures now in progress to show whether this view be correct or not: but whatever view of them be taken, the facts are sufficiently noteworthy to justify an early though incomplete record of them.

F. O. BOWER, Glasgow.

'COCO-NUT,' NOT 'COCOA-NUT.'—In the recent discussion of the subject of 'coco-nut' pearls botanists have with wonderful unanimity written the word 'cocoa-nut.' Although this is a spelling of some standing and is supported by the authority of several dictionaries it is none the less incorrect; and as botanists should be above reproach in the matter of spelling of plant-names I may contribute to

this desirable condition, so far as coco-nut is concerned, by this note in the Annals.

What is the etymological evidence? In sóme botanical works and books of travel of the sixteenth and seventeenth centuries 'coco' is derived from 'coc' or 'cocus,' a local name for the 'Indian nut,' the fruit of *Cocos nucifera*, given to it on account of a fancied resemblance of the base of the endocarp, with its three circular impressions, to the face of a monkey when it utters a cry having a sound like the words. To the Portuguese this became 'coquo,' 'quoquo' or 'coco.' De Barros, on the other hand, traces it from the Portuguese 'coco, a word applied by women to anything with which they try to frighten children,' the reference here also being to the monkey-like face at the base of the endocarp. This latter derivation is quoted by Skeat, who connects 'coco' with Lat. 'concha,' a shell, as does also Colonel Yule, who further supposes that the word may be the old Spanish 'coca,' a shell, which we have also in French 'coque.' Rumphius and others dismiss the monkey-face derivation, and suggest as the origin of 'coco' the Arabic 'gauzos-Indi' or 'geuzos-Indi,' meaning Nux Indica,' the name by which the fruit was earliest known, and 'Cock-Indi' is given as a Turkish equivalent. An old Egyptian word 'kuku' has also been mentioned as a possible source. I do not discuss here which of these derivations is the most probable; but refer to the authorities cited, especially to Colonel Yule's 'Hobson-Jobson,' for further information. That the generic name, *Cocos*, was taken by Linnaeus from the popular one will be clear upon all the evidence to any one who will look up the references which Linnaeus gives. It had been in use long before his time. Caspar Bauhin in his Pinax gives 'genera cocos seu Palmae indicae,' including under this term the date and areca-nut as well as the coco-nut palm, and other old writers also use the word with the occasional spelling 'coccos.' The latter probably gave cause for the derivation from κόκκος, adopted by Wittstein; but this is quite an untenable one.

There is nothing in any of these derivations of 'coco' to sanction the spelling 'cocoa,' and the question arises how did the mistake occur? I could not do better than apply to Dr. Murray for information on this point, and here is his reply to my question :—'The spelling "cocoa" for the *Cocos nucifera* is certainly wrong, and due merely to ignorance or confusion last century. All the people who knew wrote "coco," and only those who thought that "coco" and "cacao" were the

same, or otherwise knew imperfectly, wrote "cocoa." I cannot say absolutely who first did so; I have a quotation from Thomson's Seasons with cocoa— [Give me to drain the cocoa's milky bowl]; but I suspect (and hope) that this is only in later editions. Dr. Johnson, who rightly wrote "coco," pl. "cocoes," in his Life of Drake, written 1779, did not know the difference between "coco" and "cacao" when he made his Dictionary in 1755, and so, after explaining "cocoa" as "[*cacoatal*, Span. and therefore more properly written *cacao*]," he actually illustrates it by a quotation from Miller for *Cocos nucifera* (which Miller himself wrote "coco"), and another from Hill's Materia Medica for the "cacao" of Central America, thus identifying the two. I strongly suspect this blunder of the Doctor's was the source of all subsequent confusion.

'Bailey's Dictionary, in every edition from 1721 to Johnson's time, completely separated

"*Coco-tree*: an Indian tree, much like a date-tree, the nut of which contains a sweet substance," &c., from

"*Cocao, Cacao, Cacoa*: an Indian nut of which chocolate is made."

'Botanists and careful writers long after that stuck to "coco," as does also Tennyson in Enoch Arden—

[The slender coco's drooping crown of plumes.]

'I shall certainly use "coco" in the Dictionary, and treat "cocoa" as an incorrect by-form.'

It is to be hoped that botanists of the present day will range themselves amongst the 'careful writers' and 'those who know,' and use the correct 'coco,' for the spelling of the word has more than a purely philological interest. How many persons are there now who, like Dr. Johnson in 1755, believe that 'cocoa' (the product of *Theobroma Cacao*, L.) is derived from the coco-nut palm (*Cocos nucifera*, L.), and find in the wrong spelling an encouragement to their belief! Now too that 'coca' (the product of *Erythroxylon Coca*, Lamk.)—a word by the way which along with 'coker' and 'cocar' is found also as a variant of 'coco'—has become so important a therapeutic agent, correct orthography is even more necessary. Numerous as are the valuable properties of the coco-nut palm they stop short of supplying the beverage 'cocoa' and the drug 'coca;' and yet I have known of people who were content in the belief that this palm was the source of both of them.

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NOTICES OF BOOKS.

'DIE MORPHOLOGISCHE UND CHEMISCHE ZUSAMMENSETZUNG DES PROTOPLASMAS,' VON DR. FRANZ SCHWARZ (Separatabdruck aus Cohn's 'Beiträge zur Biologie der Pflanzen,' Bd. v. Heft 1, 1887).

In this important paper the author publishes the results of extensive and laborious investigation into the chemistry of protoplasm, and into the structure of protoplasmic bodies, such as the chloroplastid, the nucleus, and the cytoplasm.

He begins with the study of the reaction of the cell-contents. As regards the cell-sap, he points out that it is sometimes acid and sometimes alkaline,—a fact which is clearly established by the action of acids and alkalies on cells containing either blue or red cell-sap: in the former case, treatment with acid caused the blue to change to red; in the latter, treatment with alkali caused the red to change to blue; hence, the original reaction must have been respectively alkaline and acid.

The protoplasm, using the term in its widest sense, be found to be in all cases alkaline. This was ascertained by the observation both of cells containing red or blue cell-sap, and of cells with colourless cell-sap, but treated with an extract of red cabbage. In either case, when the protoplasm was killed by an electric shock, or by treatment with alcohol, or by heating, the colouring matter diffused into the protoplasm and generally gave a distinctly alkaline reaction: that is, the protoplasm stained blue, bluish-green, or green, according to the degree of alkalinity. In some cases the staining of the protoplasm was preceded by a change of colour, indicating neutralisation or alkalinity in the cell-sap. In no case did the protoplasm stain yellow, indicating a high degree of alkalinity: nor did it ever stain red, indicating acidity. These conclusions are confirmed by Pfeffer's observation[1] that the protoplasm of living cells gives an alkaline reaction with cyanin.

[1] Bot. Zeitg. 1886.

The reaction of the cell-contents, as a whole, depends upon the relative quantities of alkaline protoplasm and of acid cell-sap which are present. The alkaline reaction is most marked in young cells in which the protoplasm preponderates, the acid reaction in old cells in which the cell-sap is present in excess.

The author then proceeds to ascertain the cause of the alkalinity of protoplasm. He has recourse to analyses of the ash, and, taking leaves as giving the most reliable data, he cites a number of analyses which prove that there is a close relation between the amount of proteid in the leaves and the amount of potash in their ash. This, he believes, to be the cause of the alkalinity of protoplasm; and, after discussing the various possible forms in which potash may be present, he comes to the conclusion that it exists in combination with proteid.

The next point considered is the structure and the chemical composition of chloroplastids. After giving an account of the views of Schmitz, Frommann, Meyer, Schimper, Pringsheim, and others, as to the structure of these bodies, the author states his own conclusion, which is this: that a chloroplastid consists of a ground-substance in which are imbedded a number of fibrillae lying closely side by side; there is no definite membrane, but there is a peripheral plasma-membrane.

The colouring-matter of the plastid is confined to the fibrillæ, which are coloured green throughout; but it is especially collected into small spherical vacuoles (*grana* of Meyer).

The fibrillar structure of the chloroplastid is not apparent under normal conditions, but it becomes evident when they are caused to swell up by treatment with water. The fibrillae then swell up somewhat and separate, the ground-substance being dissolved. Hence it appears that the fibrillae and the ground-substance consist of two distinct proteid substances; the former is termed by the author *chloroplastin*, the latter, *metaxin*.

A long series of observations is given describing the effect of solutions of various salts, of potash, and of acids, upon chloroplastids. Although these are all of interest, yet it is only possible to refer to some of them. The action of potash on the colouring matter is worthy of special note. When treated with solution of potash, the green vacuoles disappear, and the whole chloroplastid becomes uniformly coloured of a yellowish green. The author considers, in

agreement with Hansen[1], that this is due to the saponification of the oily solution of chlorophyll, which constitutes the oily green drops, the 'vacuoles' or 'grana,' described above as occurring in the fibrillae. With regard to the action of strong hydrochloric acid, it is interesting to compare the author's conclusions with those of Pringsheim. The colouring matter is gradually exuded as masses of chlorophyllan (Pringsheim's hypochlorin), and the body of the plastid presents darker and lighter areas which Pringsheim interpreted as due to a trabecular or spongy structure. Schwarz, however, shows that the darker areas are granular or fibrillar masses formed by precipitation of some of the proteid by the strong acid; hence the structure of the chloroplastid is not spongy or trabecular.

Passing now to the nucleus, the author distinguishes in it the following components: a peripheral membrane, a ground-substance (*Kernsaft* of R. Hertwig), nucleoli, and a fibrillar framework. These, he finds, consist of different substances, as indicated by their reactions, which he distinguishes by various names. The substance composing the nuclear membrane is termed *amphipyrenin*; that of the nucleoli *pyrenin*; those of the framework and of the ground-substance, respectively *linin* and *paralinin*. Besides these substances there is *chromatin*, which usually occurs in the form of granules in the fibrillar framework of the resting nucleus. In the young nucleus, the chromatin is uniformly distributed throughout the fibrillar framework, though in some cases granules of chromatin are also present. This account of the chemical composition of the nucleus differs widely from that given by Zacharias[2], according to which the nucleus consists of nuclein, plastin, and albumin, the first being present especially in the chromatin-granules, the second in the framework and the ground-substance, the third in the nucleoli.

With regard to the structure and composition of the nucleus at different stages, the author points out that the framework consists at first of a single filament which, by the formation of anastomoses, forms a reticulum. This change is accompanied by an increase in size of the nucleus as a whole, due to an increase in the bulk of the framework and of the ground-substance, and, at first, to a growth of the nucleoli. But the nucleoli begin to diminish before the nucleus has completed its growth, so it appears as if the substance

[1] Arb. d. Bot. Inst. in Würzburg, III. 1884. [2] Bot. Zeitg., 1882.

of the nucleoli were used in the formation of the other portions of the nucleus. The chromatin is very abundant at first, but it does not seem to increase in proportion to the growth of the nucleus.

After it has attained its full size, the nucleus begins to diminish. The framework has either more delicate fibrillae, or some of them disappear altogether, so that the reticulum becomes much looser, and the granules of chromatin are few. In fact, all the constituents of the nucleus diminish in quantity, but no one of them disappears.

It is convenient to defer an account of the reactions of these various substances for the present, but it may be mentioned here that in some cases the author observed *complete solution* of the nucleus on treatment with water, but only in very young cells. In older nuclei the effect of water was to cause swelling-up and vacuolation, accompanied by the solution of certain of the constituents, especially the paralinin. In some cases treatment with water caused no perceptible change; this appeared to be due to the action of the tannin or acid dissolved in the cell-sap.

The author does not give any satisfactory explanation of the difference in treatment with water between young and older nuclei. The inference to be drawn from his remarks is, that the same substances are present in both, but in somewhat different forms. For instance, in controverting the conclusion of Zacharias that the nucleoli consist of albumin and plastin, the author suggests that they consist of two forms of pyrenin, one more soluble, the other less so, and that the former predominates in young, the latter in old nuclei. But this suggestion appears to beg the question. The general conclusions at which the author arrives are based mainly on the differences in solubility of the various substances which he distinguishes, and if this criterion is not admitted in this case, why should it be admitted in the others?

Coming now to the cytoplasm, the author concludes that the fibrillar structure which has been described by Schmitz and others is not normal, but is the result of precipitation or of vacuolation. In support of this view, he gives figures of precipitates obtained by the action of alcohol and other reagents on solutions of albumin, peptone, gelatin, etc., as well as of precipitates produced in both the protoplasm and the cell-sap of living cells by various chemical reagents as well as by electric shocks.

The observations on the formation of precipitates in living cells recall those made by Darwin[1] on roots and chlorophyll-corpuscles on treating them with carbonate of ammonia and other alkaline salts. Further, the fact that Schwarz obtained precipitates by means of electric shocks, suggests that the 'aggregation' induced by stimulation in the tentacle-cells of Drosera, etc. is to some extent a phenomenon of precipitation.

With regard to the ectoplasm and the 'vacuole-membrane,' Schwarz concludes that these are membranes of precipitation, and that consequently it is impossible to isolate them as distinct structures. The thick vacuole-membrane described by De Vries[2] is regarded by Schwarz as an artificial product formed on the death of the cell. The microsomata appear to consist of various different substances, and not to be structural constituents of the protoplasm.

The cytoplasm consists chemically, according to the author, except in the case of very young cells, of one proteid substance, which he terms *cytoplastin*.

Throughout the work there are numerous observations as to the physics of vacuolation which may be conveniently brought together. The author's theory of vacuolation, which is remarkably simple, is based on the fact that vacuolation only takes place in a mass consisting of at least two substances, one of which is insoluble but capable of limited swelling by imbibition, the other being soluble. He proves this by showing that no vacuolation takes place in a mass of a pure substance, such as gelatin, which is capable of limited imbibition, and this overthrows the possible view that vacuolation may be simply due to the imbibition of a larger quantity of water than the substance can retain in its molecular interstices. On the other hand, it does not necessarily follow that, in a mixture of a swelling substance, and of a soluble substance, vacuolation will be induced on the addition of liquid, as the author shows by examples. A further condition is, that the insoluble substance should be impermeable to the solution of the soluble substance. This last condition probably sets up surface-tensions which lead to the aggregation into drops of the solution of the soluble substance.

The various phenomena of vacuolation presented by chloroplastids,

[1] Journal Linn. Soc., Botany, vol. xix. 1882.
[2] Pringsheim's Jahrb. f. wiss. Bot. xvi. 1885.

nuclei, and cytoplasm, are explained on this theory by the author as follows. Treatment with water causes in many cases well-marked vacuolation of the chloroplastids; this is due to the swelling-up of the fibrillae, the chloroplastin, and to the solution of the metaxin. In some cases vacuolation does not take place because, apparently, the chloroplastin does not swell sufficiently to cause the separation of the fibrillae. That a proteid substance is actually present in solution in the vacuoles at the chloroplastids can be shown by reagents inducing precipitation, etc.

Treatment with water also frequently induces vacuolation of the nucleus: this appears to be due to the swelling of the nucleus as a whole, and to the solution of the paralinin.

The vacuolation of the cytoplasm is peculiar in that it does not appear to be due to the presence of a soluble proteid, as is the case in the chloroplastid and the nucleus—at least Schwarz failed to detect any such substance;—but no suggestion is made as to what the soluble substance may be. Vacuolation does not, however, take place in very young cells, in which the cytoplasm simply swells by imbibition; neither does it take place in old cells in which the cytoplasm is scanty, nor in cells which contain tannin; in these latter cases there is also no swelling by imbibition.

In conclusion, the chemical properties of these various substances are considered.

Chloroplastin and cytoplastin appear to be closely allied. The author rejects the suggestion of Zacharias that the plastins are identical with the insoluble nucleins, though they resemble them in some respects, on the ground that whereas these nucleins are soluble in strong potash and in concentrated hydrochloric acid, neither chloroplastin nor cytoplastin dissolve in these reagents, nor do they stain readily, as do the nucleins.

The differences between chloroplastin and cytoplastin are slight. Cytoplastin dissolves slowly in 5% disodium phosphate, and swells or even dissolves in 20% solution of the salt, whereas chloroplastin swells but little and does not dissolve in these solutions.

Metaxin appears to be an altogether peculiar proteid. Although the metaxin of the chloroplastid dissolves on treating a chloroplastid with water, yet the author doubts if it is actually soluble in water, for the observed solution may be due to the alkalies which, as has been shown, are present in the protoplasm. However, since it is stated, in

the table of reactions given that metaxin is only doubtfully soluble in dilute potash, it appears probable that it is really soluble in water. It differs from globulin and albumin in not being soluble in 10% solution of common salt, and from albuminates in not being readily soluble in dilute acids and alkalies.

Of the substances which are described as constituting the nucleus, linin and paralinin form one group, pyrenin and amphipyrenin form another, and chromatin stands by itself. They all agree in being digestible by trypsin, and differ in this respect from the plastins, cytoplastin and chloroplastin.

So closely do linin and paralinin resemble each other, that the author is doubtful if he is justified in regarding them as distinct substances. The main difference between them is that linin is not digested by pepsin, whereas paralinin is. They resemble the globulins, especially myosin, in being soluble in 10% solution of common salt, but not in stronger solutions, as also in being soluble in dilute potash;—but, unlike the globulins, they are insoluble in hydrochloric acid, whether dilute or concentrated.

With regard to pyrenin and amphipyrenin, they differ mainly in their solubility in 10% common salt solution, the former being more readily soluble than the latter, and in that the former stains whereas the latter does not. They dissolve in potash solutions, whether dilute or concentrated, and they are not digested by pepsin; they are also soluble, but not readily, in 1% solution of hydrochloric acid.

Chromatin is apparently soluble in water, but its apparent solubility when a nucleus is treated with water may be due to the alkalinity of the protoplasm. It is soluble in saturated solution of magnesium sulphate, in solutions of disodium phosphate and of common salt, and in potash, but it is not soluble in water or hydrochloric acid, nor is it digested by pepsin.

It remains to point out the relations between these substances and those which had previously been discovered as entering into the composition of the proteid molecule. According to Schwarz the proteid consists of some proteid known as protein and another, the albuminoid plastins and [illegible] ; such as albumin

Since Zacharias has shown that the [illegible]

chromatin-granules, it appears probable that it is identical with the substance which the author terms chromatin.

The author points out that the substance which Zacharias found to constitute the nuclear framework, and termed plastin, differs widely in its reactions from both cytoplastin and chloroplastin; Zacharias' nucleo-plastin is the author's linin.

The substance in the nucleus which Zacharias terms 'albumin' is apparently the same as the author's paralinin, assuming, as the author contends, that there is no albumin in the nucleoli.

The substances pyrenin and amphipyrenin, described by the author, seem to have no parallel in previous investigations.

With regard to the chloroplastids, the 'plastin' and 'albumin' of Zacharias appear to be the equivalents of the author's chloroplastin and metaxin. Similarly, in the case of the cytoplasm, Zacharias' 'plastin' is the cytoplastin of the author; the 'albumin' is recognised by both writers.

Of the substances described by the author, the majority, namely cytoplastin, chloroplastin, pyrenin, amphipyrenin, chromatin, linin, are not digested by pepsin; metaxin and paralinin being the only digestible proteids. On this ground the author refers the proteids of the former group to the class of nucleins. No one of them seems to agree in all its reactions with any form of nuclein as yet described. Hence it appears that there is no one substance which is to be regarded as nuclein proper, but that the term must be used for a class of proteids agreeing in their indigestibility by pepsin, and differing from each other in minor points.

As to the digestible proteids, metaxin and paralinin, their reactions do not identify them with any known group of proteids. Metaxin, in fact, does not appear to be allied to any of the groups of proteids, but paralinin is clearly allied to the globulins.

One general conclusion to be drawn from these researches is this, that the globulins, albumins, albumoses, etc. which have been obtained from plants are not constituent elements of the protoplasm; they are simply reserve-materials.

Since the investigation was carried out entirely by micro-chemical methods, and in view of the great difficulty of such observations, it is possible that some of the author's conclusions, especially those regarding the nucleus, may eventually have to be somewhat altered. But be this as it may, the author offers us valuable information as to

the chemistry of protoplasm, and has indicated methods by which our knowledge may be extended and confirmed. To those who are especially interested in this subject the paper cannot be too highly recommended.

S. H. V.

MONOGRAPHIAE PHANEROGAMARUM, PRODROMI NUNC CONTINUATIO, NUNC REVISIO, editoribus et pro parte auctoribus Alphonso et Casimir De Candolle. Vol. quintum, pars secunda: AMPELIDEAE, auctore J. E. PLANCHON. Parisiis sumptibus G. MASSON. Julio, MDCCCLXXXVII.

THIS is another of those valuable monographs supplemental to the Prodromus which are being issued from Geneva through the munificence and under the supervision of the De Candolles, father and son. The fifteenth family which has been thus presented, it forms a goodly part of 350 pages, completing the fifth volume of the series. The Ampelideae appeared in the first volume of the Prodromus issued by Auguste Pyrame de Candolle in 1824, and their description occupies exactly ten pages of the volume; in 1887 their treatment, even when one group is excluded, requires 313 pages. Difference in method of exposition of course accounts for some of the additional space required, and a better comparison to bring out the enormous increase in our knowledge of the group during the century is to be found in the number of species recorded in the two monographs; in the Prodromus there are 108, in the new volume 390 are pronounced certain; and there are a number of species 'non satis notae' as well.

The monograph does not include the forms belonging to *Leea* which are usually incorporated in the Ampelideae, and M. Planchon explains: 'C'est a dessein que je laisse à part les *Leea* qui forment une section très spéciale, si non une famille à part, et qui viennent d'être étudiées monographiquement par M. J.-B. Clarke, dans le Journal of Botany, new series, vol. x. (1881).' In dealing with the other forms the author differs considerably from preceding writers in his method of generic grouping. Bentham and Hooker (Genera Plantarum, i. 387) have been content to place the 230 odd species known to them in two genera, *Vitis* and *Pterisanthes*, the former including the other well-known genera *Cissus* and *Ampelopsis*, and being almost co-extensive

with the family. Most recent botanical writers have followed them in this, and the form of the leaves has been generally taken as a useful character by which species may for convenience of reference be grouped. Against this system M. Planchon utters a protest. His complaint is that single characters such as the calyptroid corolla and its pentamery and tetramery have had assigned to them too much importance, and that in consequence the apparent simplification by reduction of genera has led to confusion, and that the grouping of the species by leaf-characters violates to a great extent natural affinity. He has therefore sought for a key to the alliance of species and a natural grouping in a combination of characters taken from such features as the constitution of the disk, the form and length of the style, the relation and surface of the testa and raphe, the presence or absence of a tendril upon the rachis of the inflorescence, the form of the inflorescence itself, and the state of sexuality in the flower. Of less importance are the calyptroid form of corolla and its tetramery or pentamery, and of still less value is the form of leaf. No one of these characters is of itself sufficient to diagnose a group, but together in various combinations they mark out aggregates which he thinks may be regarded as ten natural groups. The prime value of the groups based upon these trifling characters is, he admits, open to discussion. He himself calls them genera, but others will regard them as no more than sub-genera or sections.

The scope of his genera may be best understood by examination of their conspectus :—

'CONSPECTUS GENERUM.

Flores polygamo-dioici. Petala 5 in calyptram cohærentia. Stylus conicus v. saltem brevis basique incrassatus. Stigma punctiforme v. vix dilatatum. Bacca bilocularis 2-4-sperma; semina sæpius pyriformia, foveolis ventralibus brevibus.

Frutices hemisphæræ borealis, plerisque e regionibus temperatis, fere omnes scandentes, cirrhosi. Folia simplicia, varie lobata (rarissime digitata). Thyrsi e cirrhosi v. cirrhiferi. . . . . I. VITIS Tournef. L. (pro parte).

Flores polygamo-monoici, partim pseudo-hermaphroditi. Petala 5 (rarius 4) sub anthesi patentia. Stylus brevis conicus, sæpe 10-striatus. Stigma foveiforme, vix dilatatum. Discus annuliformis erectus, sæpe 10-striatus. Bacca sæpius bilocularis, 2-4-sperma. Semina cymbiformia v. trigona, facie late bisulca. Thyrsi cirrhiferi.

Frutices scandentes, cirrhosi, utriusque orbis, plerique regionum calidarum incolæ. Folia simplicia v. palmata v. palmato-seu pedato composita.

II. AMPELOCISSUS Planch.

Flores polygamo-monoici. Petala 4-5 sub anthesi patentia. Stylus brevis. Stigma minutum. Discus annuliformis, ovarii basin cingens. Bacca bilocularis, 2-4-sperma. Semina trigono-ovata, ventre bifoveolata.

Inflorescentiæ axis in laminam lobatam dilatata, floribus in laminæ foveolis utrinque immersis, masculis marginalibus interdum pedicellatis.

Frutices Malayani. Folia indivisa vel pedato-aut palmatisecta.

III. PTERISANTHES Blume.

Flores polygamo-monoici. Petala 5, libera, expansa. Discus cupularis. Stylus longiusculus, subulatus. Bacca subexsucca, 2-locularis, 2-4-sperma. Semina ovato-trigona, ventre late bifoveolata.

Frutex Australiæ occidentalis, decumbens, cirrhosus. Cymæ pedunculatæ, basi cirrhiferæ. . . . . IV. CLEMATICISSUS Planch.

Flores polygamo-dioici. Petala 4, sæpius sub apice mucronato-corniculata, expansa. Discus hypogynus ovarii basin cingens. Stylus brevissimus v. brevis. Stigma dilatatum, 4-lobum vel 4-partitum. Bacca 2-4-sperma. Semina ovato-globosa, facie 1-3-sulca, sæpius transverse striata.

Frutices Asiæ calidæ et temperatæ, scandentes, cirrhosi. Folia sæpius pedata. Cymæ corymbiformes. . . . . V. TETRASTIGMA Miq.

Flores polygamo-monoici. Petala 5 expansa. Discus alte 5-lobus, lobi ovarii basi adnatis. Stylus brevis, crassus, cylindraceus, Stigma disciforme.

Frutex Asiæ tropicæ. Folia 3 foliolata. Cymæ corymbiformes.

VI. LANDUKIA Planch.

Flores hermaphroditi (revera nonnullis pseudo-hermaphroditis). Petala 5, sub anthesi patentia (rarius hinc inde apicibus calyptrato-subcohærentia). Discus obsoletus ovarii basi plane adnatus et tantum colore proprio subdistinctus. Stylus subulatus, crassiusculus. Bacca sæpius 1-2-sperma.

Frutices Asiæ temperatæ et Americæ boreali-orientalis, scandentes, cirrhosi, cirrhorum ramis sæpius in discum cupuliformem prehensorium dilatati. Folia digitata v. palmatilobata. Cymæ cirrhosæ. VII. PARTHENOCISSUS Planch.

Flores hermaphroditi (revera nonnullis pseudo-hermaphrod., physiologice masculis, hermaphrod. intermixtis). Petala 5, rarissima 4, sub anthesi expansa. Discus cupularis 5-rarius 4-lobus, ovarii basi inferne adnatus, sub fructu in annulum basilarem leviter accretus. Bacca 1-2-locularis, 1-4-sperma, sæpe nitore fere metallico splendente.

Frutices dumosi, cirrhosi, scandentes, non radicantes, cirrhis apice non dilatatis.

VIII. AMPELOPSIS Michx. (pro parte).

Flores hermaphroditi v. pseudo-hermaphroditi. Petala 5-7 crassa, sub anthesi patentia, post anthesim involuta, plus minus marcescentia. Discus annularis ovarii basi adnatus, sub fructu in annulum obsoletum irregulariter repandum persistens.

Frutices capenses v. Africæ tropicæ et subtropicæ, dumosi, scandentes, sæpius facie Rhois. Folia trifoliolata (foliolis externis inæquilateris) v. unifoliolata v. integra v. palmatiloba. Cymæ sæpius cirrhiferæ foliolata. IX. RHOICISSUS Planch.

Flores hermaphroditi (vel potius physiologice polygamo-monoici, floribus pluribus pseudo-hermaphroditis mascularum vicem gerentes). Petala 4, sub anthesi patentia v. interdum in calyptram plus minus cohærentia. Stylus subulatus tenuis; stigma minutum. Discus cupularis basi imâ tantum ovarii basi adhærens, margine 4-lobus. Bacca 1-2-3-4-sperma.

Frutices scandentes, repentes v. erecti, cirrhosi v. ecirrhosi, habitu et facie valde variis. Folia integra v. lobata v. varie composita (palmato v. pedato-decomposita). Cymæ oppositifoliæ v. terminales v. pseudo-axillares, raro cirrhiferæ.

X. CISSUS L. (pro parte).'

What we have here is practically this: The old genera *Vitis*, *Ampelopsis*, and *Cissus* are re-established in modified form, and from each off-shoots have been removed as new generic types. Thus *Ampelocissus* and *Clematocissus* include members lopped from *Vitis*,—the former taking monœciously polygamous forms which have non-calyptroid corollas; the latter, monotypic, having the character of *Ampelocissus*, but with a smooth long style and almost dry fruit,—and *Tetrastigma*, an old section of *Vitis* on account of its stigma, is separated as a distinct genus. *Ampelopsis* is restored in the restricted sense instituted by Rafinesque for the forms of which Michaux's *A. cordata* is the type, whilst those which are the true Virginian Creepers, and with which since the work of Torrey and Gray the genus has been so widely associated, are now separated from it as *Parthenocissus*, their obsolete disk being a chief differential character. *Cissus* has given off to *Rhoicissus* its pentamerous forms with marcescent corolla and annular disk: and lastly, *Landukia* is founded upon a single Eastern species, which has been variously referred by authors to *Vitis*, *Ampelopsis*, and *Cissus*. The larger of the genera thus created, *Vitis*, *Ampelocissus*, and *Cissus*, are divided by M. Planchon into sections.

In defence and explanation of this view of affinities in the family, M. Planchon refers in his Introduction to the relative value of the characters in which he has sought diagnostic marks and aids to generic grouping, and points out that the leaves in a family which has so many heterophyllous forms are naturally of quite secondary importance. The same may be said, though with less force, of the pentamery and tetramery of the corolla, for *Ampelocissus* has both forms in the same inflorescence. Whilst the calyptroid corolla is a general and normal feature in *Vitis*, it is present also exceptionally in *Cissus*. The constitution of the disk furnishes very important characters. Always adnate to the base of the ovary, it is erect with a distinct brim in *Vitis*, *Ampelocissus*, and *Tetrastigma*; a cup with nectariferous marginal depressions in *Cissus*; an undulate ring persisting at the base of the fruit in *Ampelopsis*; whilst it is reduced to the adnate portion without trace of brim in *Parthenocissus*. The form and length of the style are also of importance. It is conical and smooth in *Vitis*, conical and often grooved in *Ampelocissus*, and it is always short in these genera and in *Pterisanthes*. *Cissus* has a long style. *Clematocissus* is a transition form with a style almost as long as that in *Cissus*, and *Ampelopsis* has a style with the stoutness of

that in *Vitis*, only much longer. The exceptional dilatation of the stigma in *Tetrastigma* gives its essential character. The number of seeds, 1–4, in the bilocular baccate fruit serves to distinguish sections of *Cissus*, but is of less importance than the form. The structure of the seed is uniform, but the absence or presence and the length of the beak at the base of the seed, the position of the raphe on a ridge or on a flat surface, the termination of the raphe in a rounded or linear projection at a certain point on the back of the seed, together with the smooth, rough, or other character of the surface of the testa, afford characters of distinction. The presence or absence of tendrils is not a feature of much value, but the presence of a tendril upon the rachis of inflorescence is a constant feature in *Ampelocissus*, more rare in *Vitis*, frequent in South African *Rhoicissi*, and found in one Australian *Cissus*. The tendril is wanting in the inflorescence of most species of *Cissus*, *Parthenocissus*, and *Ampelopsis*. As to the inflorescence, it varies from a thyrsus in *Vitis* to a false umbel or spike or other form of cymose branching in other genera, and its kind must be taken into account as one in the assemblage of characters. The sexual states of the flower too are to be noted. *Vitis* has male flowers separate from the female ones, which latter are apparently hermaphrodite, but owing to imperfection of many flowers polygamy arises, and the genus is dioeciously polygamous; so also are some forms of *Tetrastigma*. *Cissus* has on the other hand monœcious polygamy (with appearance of hermaphroditism), and may thus be distinguished from *Vitis*.

The Ampelideae inhabit all regions of the globe save the Arctic and Antarctic[1], and M. Planchon appeals to distribution as giving support to his grouping in an interesting sketch in his Introductory chapter. The thirty-three species of *Vitis* certainly determined are confined to the Northern Hemisphere, *V. vinifera* being the only European form. Asia, which also possesses *V. vinifera*, has besides eight other species in its temperate regions (Himalaya, China, Japan). America has fifteen species, all different from those of Asia, though many are representative; for example, *V. Labrusca* of the United States and *V. Coigneliae* of Japan, *V. caribaea*, and the Indian *V. lanata*.

[1] Ventenat, indeed, named an Australian species, *Cissus antarctica*. This does not occur outside Australia, hence the name is inapt. It is not, however, without surprise that we find in this book the law of priority sacrificed before the altar of fitness, and *Cissus Baudiniana* replacing the older name of Ventenat.

Ampelocissus has sixty-two species entirely tropical, mostly African and Asian; only two are American, and one is West Indian. The eleven species of *Pterisanthes* are natives of the East Indies. *Clematocissus* is founded on von Müller's West Australian *Vitis angustissima*. *Tetrastigma*, with thirty-eight species, is entirely tropical Asian, extending westwards from India, and reaching in one species Australia. *Landukia* includes only Hasskarl's *Cissus Landuk* of Java and Tunkin. *Parthenocissus* has seven species; amongst them the well-known *Ampelopsis hederacea* and *A. tricuspidata*, which inhabit the mountainous and temperate regions of the Northern Hemisphere. To *Ampelopsis* is assigned fourteen species, false Virginian Creepers, which spread through Asia Minor, China, and Japan, and then turn up again in the Eastern State of North America. *Rhoicissus* includes the false Virginian Creepers of Africa, which, nine species in number, inhabit chiefly South Africa, but are represented throughout tropical and sub-tropical Africa by *R. erythrodes*, and in Somali Land have another representative. Of *Cissus* itself, the largest genus of the family having 214 species, the section *Cyphostemma* has its maximum in tropical and sub-tropical Africa, with a few in India and Arabia; *Cayratia* is spread in the warmer parts of Africa, Asia, and Australia; whilst the *Eucissi* are mundane in the tropics and warmer regions, but all New World species are distinct from those of the Old World.

Whilst it may be doubted whether the groups which M. Planchon has established as genera in this monograph will be accepted as such by botanists generally,—certainly those who adopt the standard laid down by Bentham and Hooker will be unable to do so,—it is impossible to estimate their value, either as a natural grouping or as a practically convenient method for identification of forms, without putting them to a practical test. The forms in the family are admittedly so variable and difficult that any scheme which provides a ready key to the species will be a boon to botanists, and it may be hoped that M. Planchon's work may supply this. Apart however from its practical usefulness in this way, the monograph, which is a worthy member of the series to which it belongs, must be regarded as a valuable contribution to our knowledge of plant-forms, for it gives the result of M. Planchon's prolonged study of living plants of the group and of his examination of dried specimens in the chief herbaria of Europe, although in regard to this latter point, it may perhaps be

matter for regret that the extensive collection at Kew and at the British Museum could only be rapidly glanced at, and that the types of Professor Lawson's monograph of the Indian forms in Hooker's Flora of British India were not examined.

I. B. B.

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The Apical Cell of Fucus[1].

BY

W. McMICHAEL WOODWORTH.

With Plate X.

I WAS induced to undertake the work, the results of which are embodied in this paper, by the state of confusion that exists in our present knowledge of the apical growth of the Fucaceae. My work was more especially stimulated by the disparity between the results arrived at by Reinke and by Rostafinski, two investigators to whom is due much of the information that we have upon the so-called apical cells of *Fucus*.

Reinke[2], whose results are based upon the study of *Fucus vesiculosus*, holds that the growing-point of *Fucus vesiculosus* consists of a group of cells uniform in structure, but that one of them is characterized by being larger than the others of the group. The protoplasm of the whole group of cells is denser than that of the other cells, and their walls are thinner. Dichotomy, or branching of the stem, according to Reinke, results from a more active growth at the edge of the growing cells; that is, cell-proliferation is more energetic at two points on the edge of the group, the points being opposite to each other in the direction of the elongated depression at the tip.

[1] The investigations of which the following pages are a record were carried on under the direction of Dr. W. G. Farlow, at the Cryptogamic Laboratory of the Museum of Harvard University, Cambridge, Massachusetts, U.S.A.

[2] J. Reinke, Beiträge zur Kenntniss der Tange, in Pringsheim's Jahrb. für Wiss. Botanik, x. (1876), p. 341. In the notes to this paper a bibliography of the older works on the subject under consideration is given.

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Rostafinski[1] also studied *Fucus vesiculosus*, and his results are the following. The vegetative point consists of a row of cells, 'Bildungszellen,' each of which has the form of a four-sided pyramid truncated at both ends. The sides of the pyramidal cells are slightly convex, and all of them are essentially of the same size, and are of equal value. The row of 'Bildungszellen' lies at the bottom of the terminal depression or pit, and is in the long axis of the same. The number of the cells varies according to age. By division in three directions these cells give rise to segments, which by secondary division are transformed into the different tissues of the plant. The segments are cut off alternately from the sides and base of the pyramidal cells.

Rostafinski holds that bifurcation of the tip takes place when the central cells of the row of 'Bildungszellen' divide into segments, and ceasing to be 'Bildungszellen' by division and proliferation, force aside the two ends of the now divided row, each end becoming a secondary row, and hence a separate growing-point.

From the above it is seen that the results of Reinke and Rostafinski are decidedly at variance. The two views agree in that the growing-point of *Fucus* consists not of a single cell, but of a group of cells. This is not in accordance with what is known of some other members of the group as shown by Kny and Valliante.

Our New England coast offers a favourable field for the study of the genus *Fucus*, from the variety of the species, and their great abundance. Most of my work was done upon *Fucus furcatus*, Ag., for the reason that my material of that species was better than any I obtained of other species. The results obtained from *F. furcatus* were confirmed by sections of *F. vesiculosus*, L., and *F. filiformis*, Gmelin.

The method used in the preparation of the material was the following. The fresh material was preserved in alcohol of about 70 per cent., and, after staining in various aniline dyes,

[1] J. Rostafinski, Beiträge zur Kenntniss der Tange. Leipzig, 1876.

was imbedded in paraffin and sectioned in ribbons on a Jung microtome, then mounted in balsam. By the ribbon method of sectioning every section was preserved, and in its proper order, a most desirable thing for the object in view.

FUCUS FURCATUS, AG.

Fucus furcatus is one of the commonest of the Fucaceae found on the New England coast north of Cape Cod; it occurs from Massachusetts Bay to Greenland. The material that I studied was collected at Nahant, in the month of February. The ultimate divisions of the frond of *F. furcatus* are more narrow than in other related species, and the midrib is much more prominent. It is characterized by the absence of vesicles or air-bladders, the great length of the receptacles, and the very regular dichotomous branching. It is found in the water at about low-water-mark, and does not occur so high up as *F. vesiculosus*.

The ends or tips of the divisions of the frond may be of two kinds. First the tips may be truncated or flattened with a depression in the centre, the depression being elongated or slit-like, the long axis of the slit being parallel to the broad surface of the frond. In other cases this terminal depression may be wanting, and in such cases the tip is conical and tapers off to a point. In the present connection I shall consider only such tips as have the depression, for the characteristic features to be described in this paper were found upon such.

If we section a tip of *F. furcatus* longitudinally, in a plane at right angles to the terminal depression, we get a state of things as shown in Fig. 1. At the bottom of the pit, which here appears as a cleft, is a large cell, appearing triangular in section, with slightly convex sides and the more acute angle directed upwards, Fig. 1, A. Immediately adjoining the large cell (in this case to the left) is another cell, smaller in diameter than the first, but equal to it in height, *A'*. A similar cell, but smaller still, is seen to the right, *A''*. Adjoining the two last-named cells there are on either side

other similar cells, and then a series of long cells. For a certain distance these diminish until they become of about a constant size, and are continuous with the epidermal cells, which dip down into the depression and together with all the cells above mentioned line the cleft, radiating as it were from the large triangular cell first spoken of.

At the bases of the large central cell and the other lateral cells are many smaller ones, somewhat irregular in shape, forming a compact mass. Lower down they are more loosely arranged, and form filaments which are the upper ends of the hyphae composing the central tissue of the stem. A number of sections parallel to this present much the same appearance, the triangular cell perhaps becoming a little smaller.

If a section be now made at right angles to the last, that is a longitudinal section in the direction of the elongated terminal depressions, and parallel to the broad surface of the frond, Fig. 2 will represent what is seen. In such a section the outline of the cavity will not have the steep sides, as in the first, but will be as a shallow depression. At the deepest part of the hollow is seen a cell (A) with convex sides and larger than any of the surrounding cells. This cell is quadrilateral, the longer axis being up and down. The general shape is oblong, the base being somewhat broader than the upper or free end. It does not differ greatly in size from the cells on either side of it, and its most prominent feature is the convexity of both the sides, while the lateral cells are convex on one side only, that being the side farthest from the central cell. The lateral cells here also form a series on either side of the central cell, growing smaller as they become more distant, and eventually merge into the epidermis. Here again, as in the last section, there is seen a compact mass of small cells about the bases of the larger ones, running into the medullary hyphae of the stem.

The central cell A in Fig. 2 is the central A in Fig. 1. The relations to the cells surrounding it are the same, the differences of appearances in form being due to the difference

in the plane of the section. As in Fig. 1, parallel sections show a similar appearance; and, assuming the sections to be of a given thickness in both cases, the characters of A in Fig. 2 are not manifest in so many sections as they are in Fig. 1.

A section made across the tip on a plane just below the bottom of the depression is shown in Fig. 3. Here is seen a series of large cells (in this case seven) A, A′, A″, etc., the central one A being more prominent than the others of the series. The cells in the middle of the series have a quadrilateral shape, particularly A. A in this section is the cell A of Figs. 1 and 2, and is seen in cross section. A does not stand out here so prominently from the lateral cells, because A′, A″, etc. are cut obliquely because they are inclined to A and not parallel with it, Fig. 2. Surrounding the central series there is a compact mass of small irregular cells.

From the three different sections through the growing-point of *Fucus* we can come to correct conclusions as to the nature of the cells and their relations to one another. The three Figures 1, 2, and 3, which represent sections through the growing tip of *Fucus*, were made at right angles to each other, and in each section there is seen a single central cell, indicated by A in all the figures, which is easily distinguished from the surrounding cells by its greater size. On comparing the different sections it is evident that this cell is shaped like a narrow wedge with convex sides and an obtusely rounded apex.

In different sections through the growing-point there is always found one cell larger than any other, and this is always situated at the bottom of the terminal depression. There is found on either side of the large cell a series of cells that become smaller as they are more distant from the central one, and in Figs. 1 and 2 they can be traced as becoming continuous with the cells of the epidermis. Besides, there are smaller cells of irregular shape at the bases of the large ones, and from them the hyphae of the stem can be seen to take their origin.

The conclusions to be drawn from the above are, that the cell A is an apical cell, the growing-point; and that from it are produced all the tissues of the plant, consisting in *Fucus* of an epidermis and a central mass of hyphae.

My studies bring me to such results that I cannot agree with Reinke and Rostafinski in believing that the growing-point of *Fucus* consists of a group of apical cells, or that there is even more than one. What I find for *Fucus* is consistent with what has been found for other genera of the order, such as *Cystoseira* and *Sargassum*, in which the growing-point consists of a single apical cell.

My figures differ so much from those of Reinke as to make explanation difficult, unless perhaps he obtained his material at a different season of the year from that in which I gathered mine.

My figure 1 agrees with Rostafinski's figure 9. In both there is the large triangular cell at the bottom of the pit, and the arrangement of the other cells is the same in each. My figures 2 and 3 correspond to figures 10 and 13 of Rostafinski. There is here a close resemblance, the essential difference being that Rostafinski makes the 'Bildungszellen' B B B etc. of equal value, while in my figure the central cell A with *convex sides* alone can be regarded as a 'Bildungszelle' that has given origin to the lateral cells A′, A″ etc., which correspond to the 'randsichtige Segmenten' of Rostafinski.

I have made a large number of sections through a great deal of material and have found this central cell with its characteristics constantly the same. It is marked by its large size, large nucleus, thin walls and denser protoplasm, and is very difficult to stain, not taking the colour like the surrounding cells.

I will now consider the relations of the *initial* cell, and the origin from it of the tissues of the plant. The series of cells on either side of the central cell are derived from it by division. These are again divided by planes in three directions at right angles to each other, the upper portions become epidermis cells and the lower or basal parts pass into the mass of

small irregular cells already spoken of which form the hyphae of the stem. The segments cut off from the sides of the initial cell may be called lateral segments. Besides the *lateral segments* the base of the apical cell is cut off, forming a *basal segment*, which by secondary division produces cells which belong to those smaller cells producing the hyphae.

Thus lateral segments of the initial cell give rise to epidermal cells and cells of the central tissue, while basal segments of the initial cell go to form cells of the hyphae only, or all of that tissue covered by the epidermis. The segments are cut off from the initial cell successively as basal, right, left, and so on, figures 1 and 2.

FUCUS VESICULOSUS, L., AND F. FILIFORMIS, Gmelin.

The facts above given for *F. furcatus* were confirmed by sections of *F. vesiculosus* and *F. filiformis*. My work was especially confined to *F. furcatus*, because of the more excellent material I had of that species.

In *F. vesiculosus* the initial cell is not so marked in shape as in *F. furcatus*, it being more blunt at the upper or free end, and on the whole more of a quadrilateral. Its large size relative to the surrounding cells is the same.

In *F. filiformis* the terminal depression is not so elongated as in either of the two other species owing to the more pointed and rounded shape of the tip. The initial cell in this species has the same characteristics as in the other two, but is, however, somewhat broader for its height.

The existence of a single apical or initial cell in *Fucus* is in every way consistent with what has been found for other members of the group by Kny[1], Reinke[2], and Valliante[3].

[1] Botanische Zeitung, vol. xxxiii. (1875), No. 27, p. 450.

[2] J. Reinke, Beiträge zur Kenntniss der Tange, in Pringsheim's Jahrb. für Wiss. Botanik, x. (1876), p. 341.

[3] R. Valliante, Fauna und Flora des Golfes von Neapel. Le Cystoseirae del Golfo di Neapoli. Leipzig, 1883.

Reinke found in *Sargassum*, *Cystoseira*, *Cystophora*, *Cystophyllum* and *Halydris*, one large pyramidal apical cell, from which are derived all the tissues of the plant. Reinke's figures 7 and 8 show the apical cell of *Cystoseira* and *Halydris*.

Valliante found but one cell for *Cystoseira*, and on plate 5, figure 2, figures the apical cell of *C. barbata* as a large wedge-shaped cell, triangular in cross section, at the bottom of the terminal depression.

Kny found one initial cell for *Pelvetia canaliculata*, a close ally of *Fucus*. He describes the apical cell as being prominent by its large size, with a broad base and the smaller end directed upwards. In cross section it appears either triangular, quadrilateral, or even square, varying in different cases. Segments are capable of further division and are cut off from the sides and base of the cell, giving rise to all the tissues. In *Fucus vesiculosus* he could not exactly determine the existence of a single apical cell, there appearing at times to be several in a row.

Thus a number of different members of this group are known to have but a single initial cell; and, should we accept the conclusions of Reinke and Rostafinski, then *Fucus* must depart widely from its allied forms. I am warranted in my belief that the structure of the growing-point of *Fucus* is essentially the same as in the other forms of the group, by the facts arrived at in my observations.

The initial cell of *Fucus*, as found by me, is a four-sided wedge-shaped cell with convex sides, the smaller, upper end being rounded and the base truncated, its greater diameter being at right angles to the broad surface of the frond.

CAMBRIDGE, MASS., U.S.A.

Fig. 1.

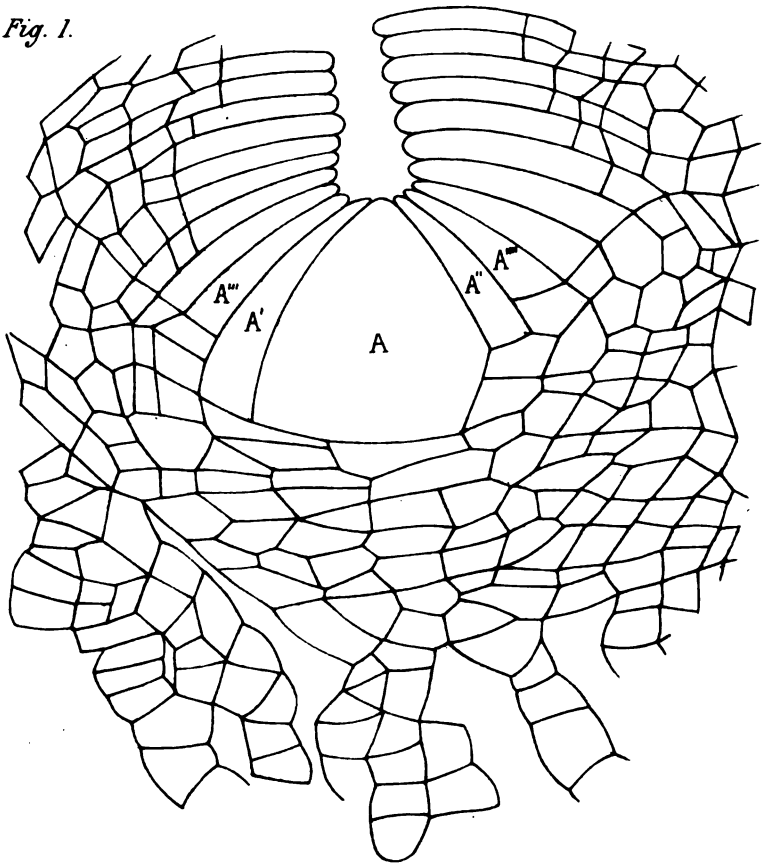


Fig. 2.

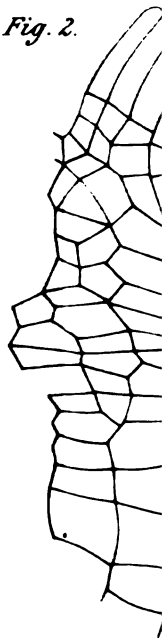


Fig. 5.

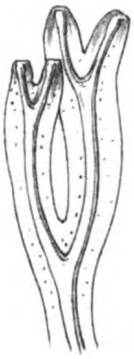
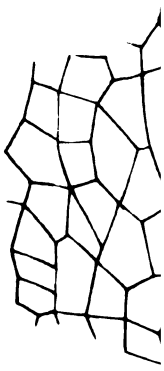


Fig. 4.



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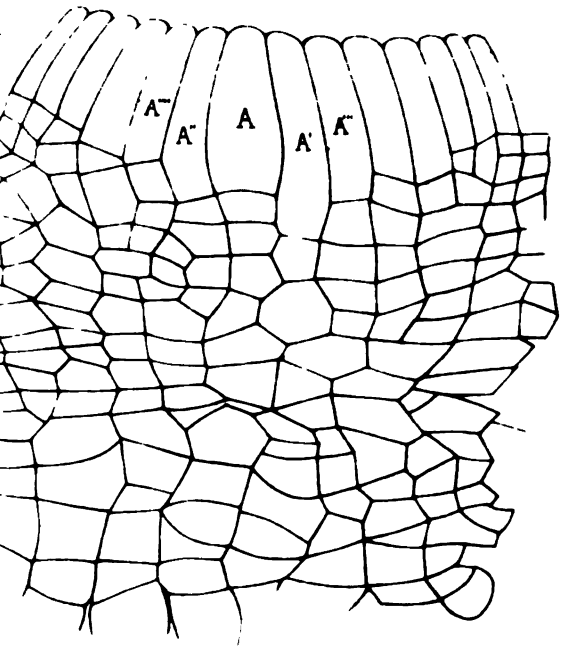


PLATE X.

Apical Cell of *Fucus*.

made at right angles
A′′′′ lateral segments

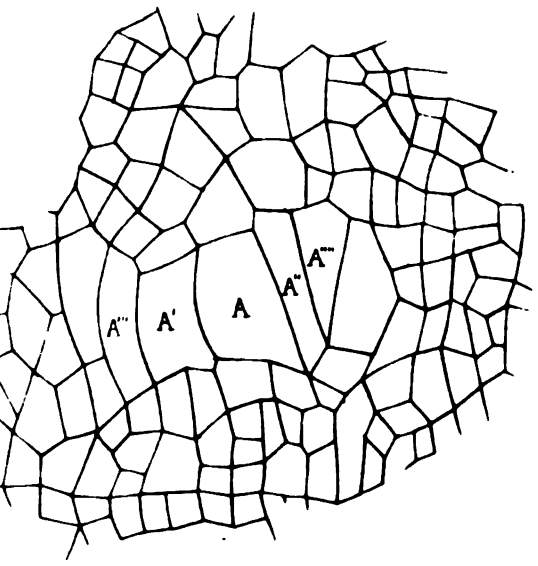
› the broad surface of

cell A is here seen in
ral cells appear larger

ıion. Somewhat dia-

ıe truncated tips con-

Fig. 3.



University Press Oxford

Fig. 1.

W M W. del

EXPLANATION OF FIGURES IN PLATE X.

Illustrating Mr. W. McMichael Woodworth's paper on the Apical Cell of *Fucus*.

Fig. 1. Section through the growing tip of *Fucus furcatus*, made at right angles to the broad surface of the frond. A initial cell, A′, A″, A‴, A⁗ lateral segments of the initial cell. × 400.

Fig. 2. Section made at right angles to the last, parallel to the broad surface of the frond. Lettering the same as in fig. 1. × 400.

Fig. 3. Section across the tip of *F. furcatus*. The initial cell A is here seen in cross section, the section being through the base. The lateral cells appear larger than natural on account of their being cut obliquely. × 400.

Fig. 4. Tip of *F. furcatus*, showing the terminal depression. Somewhat diagrammatic. × 10.

Fig. 5. A portion of the frond of *F. furcatus*, showing the truncated tips containing the depression shown in fig. 4. × about 2.

The Procarpium and Fruit in Gracilaria confervoides, Grev.

BY

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With Plate XI.

GRACILARIA is one of the many genera of the Florideae described and beautifully figured in the 'Études phycologiques' of Thuret and Bornet. In this classical work the authors describe the secondary thickening of the thallus-branches and the unusual position of the antheridia; and then proceed to discuss the structure of the mature fruits which appear on branches of the thallus as opaque, lateral, hemispherical swellings, consisting of an arched pericarp (fruit-sheath) formed by eight or ten layers of cells constituting the roof of a cavity, into which rows of spores radiate from placental cells occupying its floor; the spores subsequently escape through a pore traversing the whole thickness of the pericarp. They then speak of the procarpium as follows:—'For reasons we have given in our "Recherches sur la fécondation des Floridées," it is very difficult to find the female organ unfertilised and without a fully developed pericarp in species with opaque tissue and with fruit not localised. This is just the case in *Gracilaria confervoides*, and although the cystocarps occur along the whole length of branches, and are often very numerous, we have never succeeded in finding the procarpia, and do not know their structure. In the youngest fruits we examined, the cortical layer showed already a thickening due to the multiplication of the cells forming it.

[Annals of Botany, Vol. I. Nos. III and IV. February 1888.]

At the bottom of the thickening a small group of yellowish cells is found. Subsequently the thickened portion of the cortical layer is detached from the tissue lying beneath it, and becomes arched to form the pericarp. The group of yellowish cells grows and becomes a small hemispherical papilla in which one can distinguish two parts; a lower part, the cellular placenta, consisting of cells radiating round a basal cell with thicker walls; and an upper (more peripheral) part, consisting of smaller yellowish refractive cells, the rudiments of the spores.' The material upon which Thuret and Bornet's observations were made was collected in 1856, and up to the present time *Gracilaria* has remained one of the gradually decreasing number of Florideae whose procarpia are not known. The results I am about to describe were obtained by the examination of material which had been fixed in picric acid and preserved in alcohol by Dr. D. H. Scott, who kindly placed it in my hands nearly a year ago.

Having examined a number of the youngest fruits observable without finding a procarpium, and believing that Thuret and Bornet would not have failed to see some indication of one had it been present in like stages investigated by them, I thought that the best procedure would be to take filaments bearing the smallest visible swellings, and to make successive transverse sections of the whole filament by microtome. This was done in the case of a large number of filaments, but without any sure signs of a procarpium being seen. The work, however, was not without result, since it seemed to show that the procarpia gave external indication of their presence in the form of a swelling.

I then turned my attention to the lateral swellings, and the least of these were selected for section. The structure of the procarpium will be best understood by the examination of a few typical examples, such as those figured in Plate XI. It is to be noted that the whole of the procarpium does not lie in one plane,—a condition which increases considerably the difficulty of examining it, and of course occasions a variation in the figures according to the plane of section.

In Fig. 1 is shown a median vertical section of one of these swellings made at right angles to the axis of the branch bearing it. There is no fruit-cavity at this stage, its region of origin is indicated by the curved dotted line *f.c.* At this point the cell-walls are much swollen, and the cells exhibit a tendency to separate from one another. Outside of *f.c.* the fruit-sheath, *f.s.*, is seen. Beneath *f.c.* the group of yellowish cells mentioned by Thuret and Bornet is found, $p^1, p^2, p^3, p^4, p^5, c$. At an earlier stage in the development a single cell occupies the place of these six cells, which will be shown later to form part of the procarpium. Right and left of them come the placental cells, *p.c.* No trace of a trichogyne is visible, nor is there any sign of the pore. The fruit-cavity arises schizogenetically by the separation, owing to the splitting of their party-wall, of the two layers of cells outside and inside of the curved dotted line *f.c.* (Compare origin of conceptacles of *Fucus*[1].) The layer of cells beneath *f.c.* forms the most superficial part of the placenta, and the apical part of the procarpium.

Fig. 2 represents an older swelling. The section shown in this figure was made parallel with, instead of at right angles to, the long axis of the branch. The fruit-cavity, *f'.c'.* has begun to form. The placental cells, *p.c.*, are shown, as well as several cells of the procarpium, *p*, *p*, *c.c.*, from one of which, *c.c.*, a distinct filament, *t*, passes in a nearly straight line for some distance, then dips beneath some of the cells of the fruit-sheath, being almost lost to view in its winding course until it reappears as a small papilla, t^1, at the bottom of a conical depression on the surface of the apex of the swelling. I believe t, t^1 is the trichogyne, and that the procarpium figured here is at the stage when it is just ready for fertilisation. In this case, as in others, the procarpial cells, before fertilisation has taken place, are densely filled with finely granular protoplasm, with nuclei and leucoplastids.

Fig. 3 shows a part of a larger procarpium, the plane of section being the same as that of Fig. 2. Three or four cells of

[1] F. O. Bower, Conceptacles of *Fucus* in Q. J. M. S. 1880.

the procarpium, *p*, *p*, *p*, are very evident, of which one, *c.c.*, shows the trichogyne, *t*, growing out from its apex, which is soon lost to view.

In Fig. 4 we have another view of the procarpium. In this section the trichogyne can be traced much further than in Fig. 3, almost to the external surface of the fruit-sheath. The looseness of arrangement of the cells of the fruit-sheath in the region of the future pore, the evidence of commencing fusion of the procarpial cells, and the compressed dwindling condition of the part of the trichogyne visible, are all indications that fertilisation has taken place.

The evidence afforded by these and many other sections has led me to the following conclusions:—

1. The procarpium (using this term in its narrower sense) consists of six or seven cells, distinguished by general arrangement, size, and contents from the surrounding cells of the swelling.

2. The trichogyne arises from an apical, usually smaller, cell of this group, and after a more or less circuitous route reaches the external surface on which it projects, exposed for contact with the spermatium. The enclosed condition of the larger part of the trichogyne is counterbalanced by the projection of the whole swelling.

3. Fruit-sheath, placenta, and procarpium, all arise by the repeated periclinal division of the two or three outermost cortical layers of cells, the cells of the procarpium being early distinguishable from the placental cells by less frequent periclinal division.

4. Fertilisation takes place just after the fruit-cavity has arisen, and when only the most internal part of the pore is present.

The changes in the procarpium and placenta which follow upon fertilisation may be thus stated:—

1. Fusion of the procarpial cells with one another takes place; the placental cells may or may not multiply rapidly, forming often a large irregularly-lobed placenta, which in median sections of the swelling frequently appears bilobed,

the lobes being right and left of the depressed procarpium. In many cases the placenta remains as in Fig. 5.

2. The fused cells of the procarpium, which now have swollen walls, send out protoplasmic protrusions through these, and by means of them establish direct communication with the immediately adjacent placental cells. The protrusions are quite large enough to admit of the passage of a nucleus.

3. From the fused procarpial cells other protoplasmic protrusions (diverticula) arise, and form spores at their free ends, independently of the placental cells (Fig. 5).

4. The cells forming the free surface of the placenta develop as in Fig. 5, and produce radiating (in some cases bi- or even multi-radiate) rows of basipetally formed spores.

5. The fused procarpial cells and the deeper-seated placental cells, previously densely filled with granular protoplasm, show only peripheral layers of protoplasm enclosing large vacuoles.

Many of the placental cells may be seen, in course of these changes, with two nuclei, as if about to fuse, or as if they were sister nuclei; and, in many cases, the placental cells may be observed in direct communication with one another by protoplasmic channels, like those found connecting the procarpial with the placental cells.

Of the facts which have been observed I venture to put forward the following hypothetical explanation :—The nucleus which results from fertilisation fuses in turn with the nuclei of the combining procarpial cells. This complex nucleus then undergoes repeated division, and the daughter-nuclei pass, one through each of the previously mentioned protrusions, into the placental cells, there to fuse with their nuclei, this union being followed by division. This process occurs throughout the whole placenta, so that in the end each of the placental cells from which the spores are directly formed has received into its nucleus part of the substance of the nucleus formed by the fusion of the nucleus of the spermatium with that of the carpogenous cell. I hope by a study of living plants to test the value of this supposition of nuclear fusion and distribution.

The spores arise simultaneously from procarpial and placental cells, and by the time that they have begun to appear the pore is fully formed, and it is only in oblique sections through it that any trace of the trichogyne is obtained. The pore is formed schizogenetically, from within outwards, reminding one both in mode and in direction of origin of the formation of the pore of a stoma. The fruit-cavity arising schizogenetically increases in size lysigenetically, at the expense of the innermost layers of the fruit-sheath, the cells of which gradually lose their contents and undergo mucilaginous degeneration, the quantity of mucilage and the number of mucilage-threads of Thuret and Bornet increasing with the age of the fruit. Threads crossing the fruit-cavity, before any spores are formed, are often seen. These are not mucilage-threads, but the drawn-out ordinary floridean pit-connections of the cells which are separating to form the fruit-cavity. It is necessary to exercise care in order to avoid confounding these or the mucilage-threads with the trichogyne.

The preceding necessarily somewhat disconnected observations may be briefly and usefully summarised as follows, the order of statement corresponding as nearly as possible with the order of origin of the different structures:—The first external indication of the formation of a procarpium is the presence of a small swelling on the surface of a thallus-branch due to the repeated periclinal division of the outermost one or two layers of cortical cells. The swelling so formed consists of some twelve periclinal layers closely applied to one another, and with cells all alike, except at that point where the procarpium is subsequently found. Here, owing to the absence of periclinal division, there is one large cell full of rich granular contents. This cell, after periclinal division generally has ceased, divides near its apex, and gives off several marginal cells which arrange themselves as described (Fig. 1). At the same time the fruit-cavity begins to arise schizogenetically the fruit-sheath (pericarp, involucre) and the placental cells now full of granular protoplasm are marked off. By the time that the fruit-cavity has appeared, the end of the apical cell of

the procarpium (*c.* Fig. 1, *c.c.* Fig. 2) has grown out as the trichogyne across the fruit-cavity, and through the fruit-sheath, between its cells, to the external surface, only the most internal part of the pore being present when this occurs. Fertilisation now takes place. This act is followed by the fusion of the fertilised ovicell with the rest of the procarpial cells, the trichogyne being cut off in the usual way. The compound procarpial cell now enters into communication, by the formation of protoplasmic diverticula through its now swollen wall, with the immediately adjacent cells of the placenta. At the same time it develops at its free apex independent protoplasmic protrusions. Spores now appear with or without previous repeated division of the placental cells; the pore is fully formed; and the fruit-cavity enlarges at the expense of the innermost cellular layers of the fruit-sheath.

I must confess inability to explain the formation of the swelling by periclinal division in harmony with the theory of F. Schmitz[1], who regards all parts of the thallus of Florideae as composed of systems of branching filaments of cells. Possibly the swelling, a unique structure in the Florideae, is one of the few exceptions it is admitted may occur. The time of origin of the different parts of the procarpium in *Gracilaria* agrees with the time assigned by Schmitz as that at which the procarpium in Florideae generally developes. Following out his explanation and terminology, it may be said that in *Gracilaria* (Fig. 1) a joint-cell, p^1, produces near its apex, on one side, a two- or three-celled carpogenous branch, p^2, p^3, *c*, the apical cell of which, *c*, becomes the carpogonium (carpogenous cell), and gives origin to the trichogyne; on the other side, a two-celled branch, p^4, p^5. After fertilisation the basal part of the carpogonium is cut off as the fertilised ovicell, and combines with the auxiliary cells, p, p^1; p^2, p^3, p^4, p^5, to form one large copulation-cell, which further combines, in the manner previously described, with the surrounding placental cells—

[1] F. Schmitz, Untersuchungen über die Befruchtung der Florideen, in Sitzungsber. d. k. Akad. d. Wiss. Berlin, 1883. A translation of this paper by W. S. Dallas, F.L.S., appeared in Ann. Mag. Nat. Hist. vol. xiii (1884).

secondary auxiliary cells. In kind but not in degree this combination of ovicell with adjacent auxiliary cells is much like the mode of copulation described by Schmitz in the Rhodomeleaceae, Rhodymeniaceae, Ceramiaceae, etc.

In carrying out this investigation of the female apparatus of *Gracilaria*, I was constantly on the watch for phenomena at all comparable with those found by Thuret and Bornet in *Dudresnaya* and *Polyides*[1], by Berthold in the Cryptonemiaceae[2], by Schmitz in the Squamarieae[3], and by Solms-Laubach in the Corallinaceae[4]. Each fruit was however found to be the direct product of a procarpium, and each procarpium gave one cystocarp, and one only. Still, from one point of view, *Gracilaria* shows a combination of the salient features exhibited in the production of the many connected, scattered fruits of the Cryptonemiaceae, and of the single compound fruit of the Corallinaceae. In describing the parts in *Gracilaria*, I have, as far as possible, used the terms (and with the same meaning) proposed by Schmitz[5] and adopted by Berthold. In *Gracilaria* the fertilised ovicell fuses with the rest of the procarpial cells, the auxiliary cells, homologous with the single auxiliary cell of, say, *Gloeosiphonia*; the placental cells correspond with the isolated fertile auxiliary cells, from each of which by contact with the connecting 'tubes' a fruit is formed in the Cryptonemiaceae and Squamarieae. In *Gracilaria*, owing to the concentration of the auxiliary cells (placental cells) round the procarpium, there is no need of these long cellular connecting-tubes, and they are replaced by the protoplasmic protrusions mentioned. The formation of a single compound fruit in the Corallinaceae as a result of the fusion of a group of procarpia, only some of which are fertilised, is not unlike the formation of the single complex fruit of *Gracilaria* as the product of the more or less intimate fusion

[1] Thuret and Bornet, Études phycologiques, pp. 73–80.
[2] G. Berthold, Die Cryptonemiaceen des Golfes von Neapel, 1884.
[3] F. Schmitz, op. cit. on page 219.
[4] Solms-Laubach, Fauna u. Flora des Golfes von Neapel, 1881.
[5] F. Schmitz, l. c., p. 223.

of the single fertilised procarpium with the surrounding placental (auxiliary) cells. Indeed, much of the description of the development of the fruit of the Corallinaceae by Schmitz, but not by Solms-Laubach, will apply equally well to *Gracilaria*. The place of origin of the spores of *Gracilaria* represents a combination of the condition seen in the Helminthocladieae—the simplest of the Florideae, in the Ceramiaceae, and in the Cryptonemiaceae—the highest of the Florideae.

Gracilaria, in its female apparatus, seems to stand in the same relation to the rest of Florideae as *Chara* does to the rest of Chlorophyceae. In most of the higher Florideae the procarpium, after fertilisation, becomes enclosed in a cellular sheath derived from the adjacent cells of the thallus. An envelope, similar in time and place of origin, and in function, is found in most of the Coleochaeteae amongst the Chlorophyceae. In *Gracilaria*, as in *Chara*, this cellular sheath is formed before fertilisation, a mark of greater specialisation. In a subsequent paper I hope to give an account of the procarpium and fruit of *Sphaerococcus*, of the family Sphaerococcaceae, in which *Gracilaria* is placed.

I must not conclude without acknowledging my indebtedness to Dr. D. H. Scott, for his suggestion of this work and for kindly criticism during its progress. I would also take this opportunity to thank Mr. Thiselton-Dyer for the use of the Jodrell Laboratory, Kew, in which the greater part of this investigation was carried out.

EXPLANATION OF FIGURES IN PLATE XI.

Illustrating Mr. T. Johnson's paper upon the procarpium and fruit in *Gracilaria confervoides*, Grev.

Fig. 1. Vertical median section of swelling made at right angles to axis of thallus-branch bearing it. *f. s.* fruit-sheath. *f. c.* curved dotted line, representing line of origin of fruit-cavity. p, p^1, p^2, p^3, p^4, p^5, procarpial cells. *c.* carpogonium. *p. c.* placental cells. × 600.

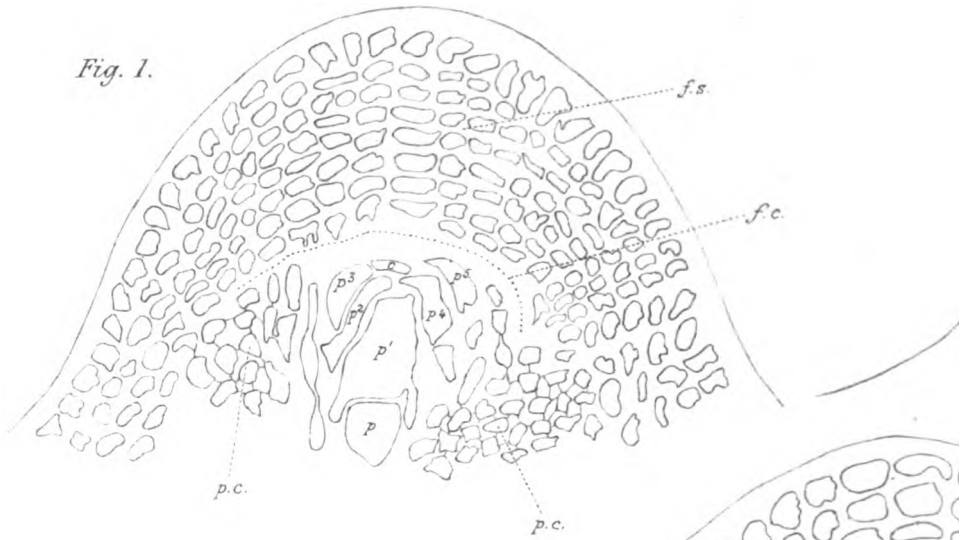
Fig. 2. Vertical median section of the swelling made parallel with, instead of at right angles to, the axis of the thallus-branch. Older than section in Fig. 1. *t*, *t'*, trichogyne. *f'. c*. fruit-cavity; other letters as in Fig. 1. Procarpium ready for fertilisation. × 600.

Fig. 3. Vertical median section of swelling in same plane as in Fig. 2. Lettering as before. Procarpium larger. Before fertilisation. × 600.

Fig. 4. Vertical median section of the swelling in same plane as in Fig. 1. Lettering as in Fig. 1. Procarpial cells fusing. After fertilisation. × 600.

Fig. 5. Vertical median section of the swelling in same plane as in Fig. 1. *s* spores; other letters as in Fig. 1. Pore complete. × 600.

Fig. 6. Same section as that in Fig. 5, magnified only five times in order to show the size of swelling relatively to thallus-branch, the structure of which is indicated. × 5.



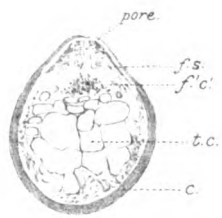


Fig. 6.

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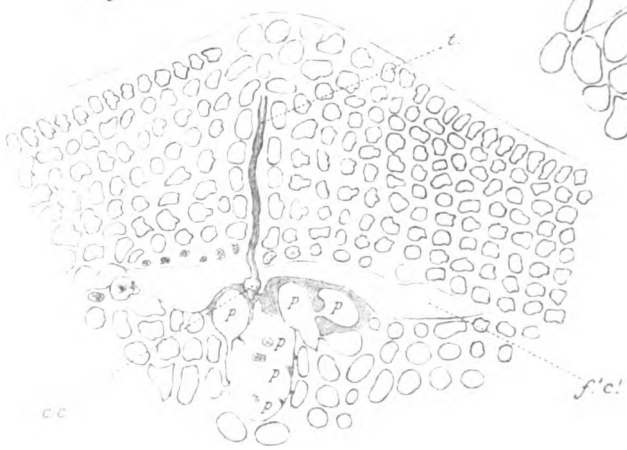
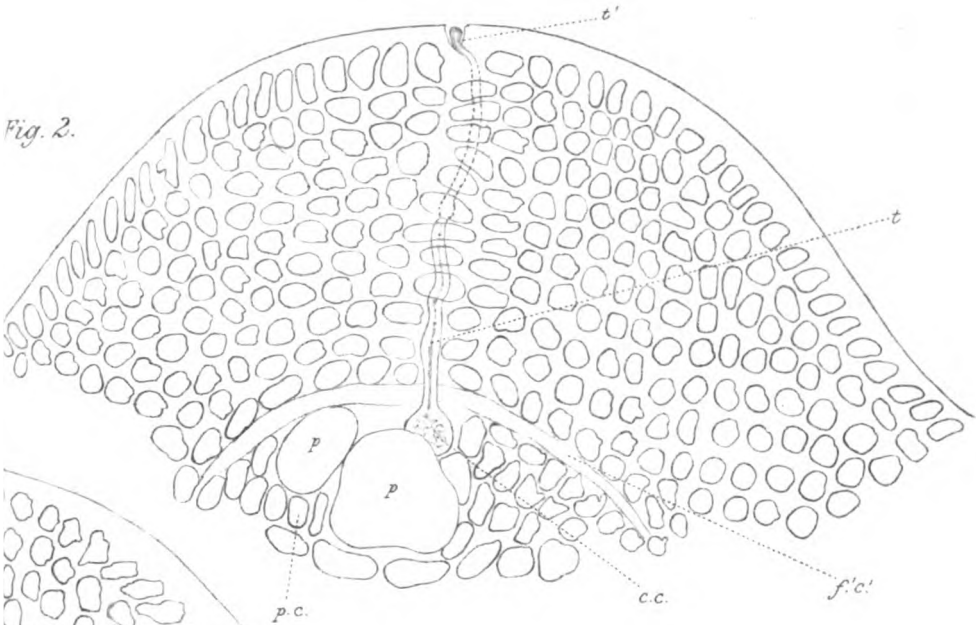


T. Johnson del.

JOHNSON.—ON THE FRUIT IN GRACILARIA CONFERVOIDES, Grev.

Fig. 2.



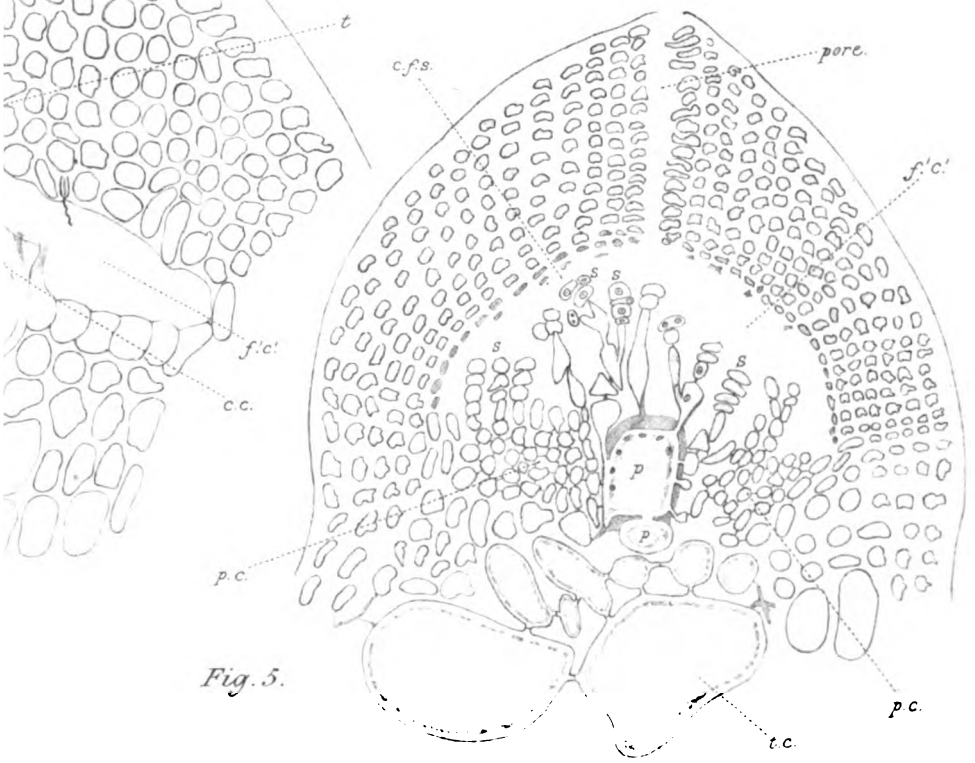


Fig. 5.

University Press, Oxford.

On the germination of the tuber of the Jerusalem Artichoke (Helianthus tuberosus).

BY

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Professor of Botany to the Pharmaceutical Society.

A GROUP of plants, prominent among the Compositae, store their carbohydrate reserve-materials in their tubers or tuberous roots in the form of inulin. Of these plants the dahlia (*Dahlia variabilis*) and the Jerusalem artichoke (*Helianthus tuberosus*) are most frequently met with. In the somewhat fleshy, though not tuberous, roots of the common species of *Inula* (*I. Helenium* and *I. Conyza*) a similar accumulation may be found.

Inulin can be prepared from these plants by boiling the tubers, or roots, with large quantities of water, concentrating the decoction so obtained, and allowing it to stand till it deposits a sediment. This is to be redissolved in a small quantity of hot water, decolourised by boiling with animal charcoal, and again concentrated, when it gradually deposits fairly pure inulin. This can be purified by redissolving and evaporating again till the inulin is precipitated, when it should be well washed with cold water containing a little alcohol. In the tuber the presence of inulin can be detected by soaking pieces in alcohol for two or three days and cutting sections. These, dipped in water and examined, show large sphaero-crystals of inulin deposited in the tissue, which often embrace several cells within their area.

Inulin, prepared as described above, is a white powder which is readily soluble in warm water, dissolves only slightly in cold water, and is insoluble in alcohol. It is not thrown down

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from its watery solution on cooling, so that the latter can be diluted to any desired degree. It is precipitated on adding alcohol in sufficient quantity to the solution.

Its relation to sugar is very much the same as that of starch, for it is readily converted into sugar by boiling with acids, or by heating its watery solution under pressure[1], the change being probably one of hydration, just as is the case with starch. Its formula, according to Watts' Dictionary of Chemistry, is $C_{12}\ H_{20}\ O_{10}\ 2H_2O$. It differs from starch in not occurring in the form of grains of definite shape, but being crystalline when isolated, and occurring in solution in the sap of the cells which contain it. Further, it differs from starch in resisting to a very large extent the action of saliva[2], and in being capable of dialysing through a moist membrane. This power however is very feeble. Like starch, it has an action on polarised light.

In the plants spoken of, inulin does not replace starch altogether, for the latter is found in the sub-aerial parts, but it is the only form of carbohydrate reserve-material.

The chemical changes in the reserve-materials accompanying germination have in many cases been shown to be due to the action of different unorganised ferments. There is no doubt that starch is changed into sugar by a body of this description, to which the name of *diastase* has been given, and which has been shown by different writers to occur in almost every growing part of green plants. The changes brought about in the different proteid reserve-materials have by several observers been shown to be due to a similar cause[3], and cellulose is demonstrated to give rise to sugar by the same agency[4]. Prantl[5] and others have shown that sugar is formed from inulin, and in investigating the peculiarities of this change the first question that suggests itself is,—Is the conversion due,

[1] Poulsen, Bot. Microchem. p. 88.

[2] Cf. infra.

[3] V. Gorup-Besanez, in Ber. Deutsch. Chem. Gesell. 1874, p. 1478. Green, in Phil. Trans. vol. 178 (1887) B, p. 39.

[4] Green, op. cit.

[5] Prantl, Das Inulin, 1870.—Sachs, Lectures on the Physiology of Plants, Engl. ed. p. 343.

as in so many other cases, to an unorganised ferment? Sachs concludes that this is the case, and that the ferment resembles invertin. He does not, however, quote any experiments on the point.

The material used for the investigation was the tubers of the Jerusalem artichoke (*Helianthus tuberosus*). Examination of the young shoots and roots arising from the germinating tuber showed that, while inulin was present in them, there was a far larger proportion of sugar there also than was present in the tissue of the resting artichoke. Inulin, as has been mentioned above, is known to be capable of conversion into sugar, and therefore the abundance of the sugar in these parts suggests that it has arisen at the expense of the inulin, and that consequently in the germinating tuber something may be looked for capable of converting the one into the other. The sap of the tuber when expressed was nearly neutral; with very sensitive litmus paper a trace of acidity could be detected, but so little as to negative the idea that the conversion was brought about by the instrumentality of an acid. The probability of the conversion being due to a ferment-action was at once apparent.

Tubers of the artichoke were planted and allowed to germinate till the young plants arising from them had attained a height of about six inches above ground. The tissue of the tubers was now found to have become much altered, the interior having become spongy and the cells almost empty, while on the outside and for some distance inwards it was firm and succulent. Microscopic examination showed the cells of this outer part to be filled with colourless cell-sap, from which by appropriate treatment the well-known sphaero-crystals of inulin could be separated out. There was a considerable quantity of sugar present, but no starch, neither extract nor sections giving any reaction with iodine. The tubers were minced finely and extracted with glycerine, in which inulin is insoluble. After twenty-four hours the glycerine was strained off and the extract dialysed till the dialysate failed to reduce Fehling's solution.

The subsequent experiments with such a glycerine extract

were carried out, some in test-tubes, and others in parchment dialysers. In the latter cases the dialysates were tested for sugar as the action went on, its presence being taken to indicate a formation of it, as the solution of inulin which was used to test the power of the glycerine-extract was itself dialysed carefully before use, so as to prevent the possibility of the introduction of any sugar during the preliminary operations. The dialysates were changed at intervals of twenty-four hours. In all cases careful control experiments were made with boiled extract, in order to confirm the view that any changes occurring were due to the action of a ferment. The weather being extremely sultry, precautions were taken against the appearance of bacteria by using thymol in all the experiments.

Particulars of two typical experiments are subjoined.

Experiment 1, carried out in test-tubes :—

A contained 10 cc. dialysed extract + 15 cc. inulin solution.

B contained 10 cc. dialysed extract boiled + 15 cc. inulin solution.

A trace of sugar was present in the extract, but not much. Action began gradually, and proceeded slowly and regularly for several days, the difference between the contents of the tubes when tested with Fehling's solution becoming more and more marked as the digestion proceeded. After six days the contents of B gave no more reduction than at first when boiled with Fehling's fluid, while those of A gave a vivid red under the same conditions.

Experiment 2, carried out in dialysers :—

A contained 40 cc. of inulin-solution (1 per cent.) + 5 cc. extract of tubers.

A_1 contained 40 cc. of inulin-solution + 5 cc. extract boiled.

Again there was a small amount of sugar present in the extract.

In two days the dialysate of A had a greater reducing

power than that of A_1, the latter only showing what was due to the sugar in the extract. The dialysates were changed and the dialysis continued for twenty-four hours longer, when the difference in favour of A was very marked, the control showing the presence of a mere trace of sugar.

The same results were arrived at in other cases, the details of the experiments, as to the relative proportions of inulin and extract used, being varied in many ways.

Coincidently with the appearance of the sugar in the dialysates, the amount of inulin in the parchment tubes underwent diminution. The amount of precipitate thrown down by alcohol from the fluid containing the unboiled extract of the tubers became less and less as time went on, measured quantities being taken for that purpose. Similar quantities taken from the controls showed no such diminution.

These results establish the presence of a ferment in the germinating artichoke, by whose instrumentality inulin is transformed ultimately into some form of sugar. The time taken up in the experiments is to be accounted for possibly by the very small quantity of the ferment present, and its dilution in the process of extraction. In the artichoke it is probable that it only exists at any particular time in the cells whose contents are being changed into sugar, and as it takes several weeks for this conversion to be brought about in any tuber, there must be but little ferment to be found at any one moment. Some experiments bearing on this point will be detailed later on.

Like so many of the digestive ferments, both animal and vegetable, the ferment brings about a change which is quite easily caused by other means. The action of acids at a boiling temperature has already been referred to. Besides this I found that prolonged exposure to dilute acids at the ordinary temperature, and still better at about 40°C, is capable of bringing about the same conversion. Alkalis on the other hand have no action on it. Prolonged suspension in cold water will also transform some inulin into sugar, though the energy of water is very feeble compared with that of acid.

Still I always found that any solution or suspension of inulin that had been standing for some weeks contained a trace of sugar. This fact at first was very disturbing, but its importance was minimised by having very careful control experiments always carried out side by side with the others during the whole investigation.

The effect of the ferment is therefore in this, as in so many other cases, to bring about more quickly an effect that can be caused by other agencies.

The ferment so demonstrated is distinct from the ordinary diastase which transforms starch into sugar. An experiment on this point is subjoined.

Large test-tubes were taken and treated as under :—

A contained 10 cc. glycerine-extract of tubers + 15 cc. inulin-solution.

B contained 10 cc. glycerine-extract of tubers boiled + 15 cc. inulin-solution.

C contained 10 cc. glycerine-extract of tubers + 15 cc. one per cent. starch-paste.

D contained 10 cc. glycerine-extract of tubers boiled + 15 cc. one per cent. starch-paste.

The tubes were then put in a water bath at 35°C. A gradually and regularly showed an increase in the amount of reduction noticeable on boiling with Fehling's fluid, while B, C, and D remained exactly as at first for four days. The ferment is therefore not diastase.

It is interesting to note here that while the inulin-ferment is not able to act upon starch, saliva, which is so energetic with the latter, has little or no power to convert inulin. In two experiments upon this point I subjected inulin to the action of saliva for twenty minutes and for twenty-four hours respectively, and got no perceptible amount of sugar formed in either case. That the saliva was active I proved by having control tubes containing starch, which were treated exactly like those containing inulin, and these showed conversion proceeding at the normal rate.

The conditions of the activity of this inulin-ferment are similar to those which govern the digestive ferments of the animal organism. Like saliva it works best in a neutral medium. The presence of a very slight trace of acid does it no harm; in fact it is rather advantageous. The sap expressed from growing tubers is very faintly acid, the acidity being equal to about ·001 per cent. of HCl. Stronger acids than this are prejudicial, and exposure for an hour to an acidity equal to ·2 per cent. of HCl at a temperature of 40° C destroys it altogether. Alkalis are similarly hurtful, no ferment-power surviving an exposure for an hour to a strength equal to 1·5 per cent. of $Na_2 Co_3$ solution. The rapidity with which the destruction of the ferment by acid takes place is dependent on the temperature at which it is kept during the time the two are in contact. At a low temperature it is much less affected than at 40° C, but after an hour's exposure at 10–15° C its working power is very much impaired.

The energy of the ferment shows the same variation with the temperature, being much greater at 40° C than at the ordinary temperature of the soil in which its normal action takes place. The same thing I have noted elsewhere[1] is the case with the proteolytic ferment occurring in the lupin. It is destroyed by boiling.

The products of the action of the ferment on inulin are a sugar and an intermediate body possessing properties which resemble those of inulin on the one hand and sugar on the other. In the first stages of this investigation, formation of sugar was, as already indicated, taken as the sign of the activity of the ferment extracts. The products of the digestion were collected later for more exact enquiry into their composition. To obtain them digestions were conducted for some days in dialysers; the first three days' dialysates were rejected, to be sure that whatever was examined was really the product of the ferment's action and not any dialysable matter possibly mixed with the inulin; the later dialysates were

[1] Phil. Trans., vol. 178 B, p. 46.

collected and concentrated over water baths till of very small bulk, when they had a syrupy appearance and consistency.

These concentrated dialysates were found to contain three bodies that could be separated from each other by treatment with alcohol. The first of these was a sugar, and was separated by extracting the syrupy residue with absolute alcohol, when about half of it dissolved. On decantation from the undissolved residue, and concentration over a water bath, this again became syrupy, and remained so, refusing to crystallize, even when exposed over strong sulphuric acid. It was freely soluble in cold water, and its solution reduced Fehling's fluid when boiled with it. As I was unable to get it into crystalline form, I could not determine its specific rotatory power. It had a feebler reducing power than dextrose or laevulose, and this power was considerably increased by boiling it for a few minutes with about two per cent. of HCl.

Having extracted this sugar from the concentrated dialysates by treatment with absolute alcohol, there remained a residue about equal in bulk to the sugar taken up. A great deal of this dissolved freely in cold water, which is not the case with unaltered inulin. The rest remained insoluble till heat was applied. This consisted of inulin that had dialysed through the parchment during the later stages of the digestion. An experiment was conducted on this power of dialysis, some inulin-solution, without any ferment, being dialysed in a fresh well-tested parchment tube for several days, when the dialysate, on being concentrated, deposited a residue which the microscope showed to consist chiefly of the well-known sphaero-crystals of inulin.

The two constituents of the residue, after separation of the sugar, were separated from one another by treatment with alcohol. Careful experiments showed that inulin was insoluble in alcohol of sixty-five per cent. strength. On making the solution of the residue up to this strength of spirit, there was a precipitate which gradually separated out and settled to the bottom of the fluid. On filtering and adding further alcohol, no change took place till about eighty-two per

cent. of spirit was present. Then opalescence set in again, and gradually a very finely-granular precipitate separated out, one much more finely-granular than the first one. This consisted of the intermediate body, which had been found to be soluble in cold water. In 100 parts of the residue there were about 62·5 parts of inulin which had passed the dialyser unchanged, and 37·5 parts of the second body.

On concentration of the watery solution of this residue it deposited sphaero-crystals of inulin and a quantity of other crystalline matter. These crystals appeared generally as plates, sometimes pentagonal, sometimes rhomboidal or oblong, with here and there needle-like prisms forming part of a rosette. They could under the polarising microscope be readily distinguished from those of inulin, the latter not being so strongly doubly-refractive, and having the form of circles showing the cross so characteristic of the sphaero-crystal. The others were probably due to the intermediate body.

Some samples of inulin contain a certain portion of this body, which can be separated from the inulin by fractional precipitation with alcohol, as already described. In one sample I tested there was 12–14 per cent. of it. It has a greater power of dialysis than inulin has, but to separate it by this method is not easy. In the case of some of the last-mentioned sample of inulin, when the dialysate was concentrated after the process had gone on for five days, this intermediate body formed sixty-six per cent. of the total precipitate which could be thrown down by alcohol.

This product then differs from inulin in the following particulars:—

1. It is more soluble in cold water.
2. It has a greater power of dialysis.
3. It has a different crystalline form.
4. It is soluble in alcohol of sixty-five per cent. strength, not being precipitated by less than eighty-two per cent.

Returning to the experiments quoted on p. 229 it is clear that this body occurred in the dialysates in consequence of its

formation during the digestion and not from having been present in the inulin used, for the dialysates of the first three days were rejected. If any had been mixed with the inulin taken for experiment this would have escaped during that time, as its dialysing power is so great compared with that of inulin. Its occurrence as a consequence of the action of the ferment recalls the occurrence of dextrin during the action of the ordinary amylolytic animal ferments. The body too somewhat resembles dextrin, being soluble in stronger percentages of alcohol than the original carbohydrate, but not soluble in a greater percentage than eighty-two, at which point dextrin also is precipitated. Unlike dextrin, it gives no reaction with iodine, but this is not remarkable, as inulin differs from starch in the same respect.

The slowness with which the ferment-extract was found to work is probably due to there being an extremely small quantity present at any particular time. The progress of germination in the tuber of the artichoke is extremely slow and gradual. As the plant continues to develop, the tuber becomes more and more exhausted, but it contains inulin for months, until in fact the new tubers are being formed on the underground stems that have been developed from the parent tuber. The interior is the first to be exhausted, the outside often continuing hard and succulent till it is only a thin shell, while the inside is spongy and dry. The ferment is only to be looked for at any moment in the cells which are parting with their carbohydrate contents.

It cannot be found at all until the young stems begin to emerge from the tuber, and then its presence is maintained till the store of inulin is all exhausted. The quantity that can be extracted from the minced tubers is small, for a single digestion with glycerine takes it nearly all up, hardly any being found in a subsequent extraction. An examination of the plant while the germination is going on enables the course of events to be followed fairly well. In the resting tuber before germination begins, the inulin is found to occupy nearly all the cells in its interior, which consist almost entirely of paren-

chymatous tissue, the fibro-vascular tissue being extremely reduced. The microscopical tests for inulin are very imperfect, depending on precipitation in particular forms by alcohol or glycerine and chiefly on the occurrence of the well-known sphaero-crystals. In working at the micro-chemical reactions of inulin I was however fortunate in finding a test which always indicated it when present and enabled me to see exactly where in the sections the cells contained it. This was a solution of orcin in alcohol. On warming with strong HCl a section soaked in this reagent, the cells containing the inulin were stained a deep orange-red. The commercial preparations of inulin which I had gave the reaction in a very marked manner, and on treating, in the way described, sections in which the sphaero-crystals had been deposited, these dissolved leaving an orange-red area which they had occupied.

I found too that solutions of inulin boiled with strong HCl, to which a little orcin in alcohol had been added, took on this deep orange-red tint. Phloroglucin was as efficacious as orcin, the colour being rather more brown. On the tube cooling the clear orange-red colour was replaced by a brown precipitate. In tracing the progress of the inulin I used the orcin-reaction.

As the young stem grew, the inulin could be seen to follow its increase in length, occupying the centre of the shoot, and leaving the circumference free. It did not reach so far upwards as the growing-point but stopped abruptly just behind the actively growing zone, so far as I could make out. It was accompanied in its progress by sugar, which extended rather further forwards, but which also could not be detected with certainty in the growing-point. This agrees with observations which have been made in the cases of growing-points supplied with sugar at the expense of starch. From the power of dialysing which inulin has been shown to possess, this travelling of it towards the growing-point does not seem remarkable. Its occurrence just behind the growing cells may be due to an actual transit of the stored inulin before

being converted into sugar, it being thus brought near to the point where it is changed. On the other hand, it may with greater probability be suggested to have another origin altogether, and to be caused by the supply of sugar being too rapid for the needs of the growing cells. The surplus sugar might in such a case be reconverted into inulin temporarily, till wanted. Such reconversion is a matter of constant occurrence in the case of supplies of starch.

Should the first-mentioned view of its presence be the correct one, and the inulin itself be able to travel from the tuber to the growing-point, it suggests the question of the necessity of any ferment-transformation. But the easy transport of the carbohydrate-material is only one of the requisite conditions of the nutrition of the growing cells. We can hardly suppose, at any rate in the case of inulin, that it is transformed into sugar merely to be more easily moved about the plant. There still remains the question of the condition in which the carbohydrate must be to serve as nourishment to the cells of the growing-point. This must apparently be sugar, and hence we have always sugar supplied to the growing tissue.

I have said above that the presence of the ferment is only to be expected where the carbohydrate material is being rendered available for use. It follows from this that it should not appear in the tubers till the onset of germination, and that consequently in a resting tuber none should be discoverable. In an experiment on this point some developing tubers were taken from the plant on which they were being formed, and their stalks carefully cut off close up to the tubers, so as to leave nothing but the latter. These were then mashed up carefully and covered with glycerine. After two days' exposure to this liquid, the extract was filtered off. It was found to contain a good deal of sugar. Two dialysers were prepared, A and B. In A were put 10 cc. of this glycerine-extract and 30 cc. of inulin-solution. B was made up similarly, but the extract was well boiled before adding it to the inulin. Outside the dialysers 200 cc. of water were placed. As sugar dialyses rapidly through parchment-paper, the dialysates were changed

frequently, and were tested carefully at intervals to see whether any difference of reducing power between the two dialysates could be detected as time went on. After three days both the dialysates were quite free from sugar, and during this period there was never any difference of reducing power to be observed. Had any ferment been present in the extract, the dialysate of A should have given evidence of its activity by an increased reducing power, but of this, as I have said, there was no indication. The sugar originally present in the extract was equally present in both dialysers, and it gradually dialysed out at the same rate in both. When this quantity had disappeared, there remained nothing in A that would reduce Fehling's fluid, as there would had ferment been present. Both dialysers at the end of the experiment contained nearly as much inulin as at first, only a little having dialysed out during the experiment. Hence no ferment is present in the developing tubers.

There remains for consideration the condition in which the antecedent of the ferment exists in the tubers till the onset of germination. From analogy with other ferments, both animal and vegetable, it appears probable that it is present in the form of a zymogen. In many cases this can be proved to be the antecedent form of ferment, as e.g. in the gastric and pancreatic glands in the animal body. An extract of these glands, taken while they are quite fresh, is found to possess no digestive powers, but to become active when warmed with a weak acid. A gland that has been kept warm for some hours before the extract is made is found to contain large quantities of the ferment. My first experiments on this point were made with very small tubers, and were not conclusive. Later in the year I was able to use tubers that had attained their full size, and with these I was more successful.

Some full-grown artichokes were procured; half of them were at once extracted with glycerine, as in the other cases described. The remainder were sliced each into about four pieces, and were put into a beaker over a bath at 35° C, and kept there for twenty-four hours, after which they were minced,

and an extract made, as in the other case. The first of these two extracts proved to be quite inert, while the second showed a power of converting inulin into sugar. The experiments were carried out as before in well-tested dialysers, the dialysates being examined at intervals for sugar.

I was unable to obtain any evidence of the formation of ferment in the extract of the unwarmed tubers by the action of acid alone. I tried hydrochloric, acetic, citric, and malic acids, but none had any effect. This might be due to the destruction of the ferment by the acid as fast as it was formed, for it is most sensitive in this direction, as already pointed out. When the extract was treated with a solution of acid-albumin in ·2 per cent. HCl it did give rise to a certain amount of ferment, though less than was obtained by warming the tubers for twenty-four hours before the extract was made.

The result of the investigation into the germination of the artichoke tuber may be briefly summarised as follows:—

1. The stored inulin in the tuber is made available for the use of the plant by ferment-action.

2. This ferment is not diastase, but a special body working on inulin.

3. Its action is to produce from the inulin a sugar and an intermediate or collateral product.

4. The latter differs from inulin in its solubility in water and alcohol, its crystalline form, and its power of dialysis.

5. The ferment does not exist as such prior to the commencement of germination, but is present in the resting tuber in the form of a zymogen, from which it can be developed by the action of warmth, or, under certain conditions, by that of acid.

6. Its activity is only manifested in a neutral or very faintly acid medium, and it is destroyed by prolonged contact with acids or alkalis.

On the Sensitive Labellum of Masdevallia muscosa, Rchb. f.

BY

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With Plate XII.

THE irritability of the labellum in certain orchids would appear to have been discovered by Robert Brown about 1830—in the first instance for *Pterostylis*, and to have been communicated by him to Lindley. In his Vegetable Kingdom[1] Lindley quotes the following orchids as possessing irritable labellums:—*Pterostylis*, *Megaclinium*, and *Caleana nigrita*, in each case the contractility residing in the narrowed hinge or neck.

It is however a mistake to include *Caleana* in this category; for Fitzgerald[2], in a most careful and intelligent account of the mechanism of this orchid, conclusively shows that the motility of its labellum arises solely from the great flexibility of its narrowed hinge. In this flower, by inversion, the labellum stands above the column. An insect alighting on the under (i.e. side towards column) surface of the labellum drags this down with it and becomes shut into the cup-like column, the labellum forming a close-fitting lid. It is no case of irritability.

Megaclinium falcatum was the subject of one of Ch. Morren's classical memoirs[3]. The movement here is entirely spontaneous (as in *Desmodium gyrans*), and consists of a slow oscillation in a vertical plane. Mechanical stimulation has no effect. In *Pterostylis* the movement of the labellum is

[1] Ed. 1853, p. 179.

[2] R. D. Fitzgerald, Australian Orchids, vol. i. Sydney, 1882.

[3] Ch. Morren, Recherches sur le mouvement et l'anat. du labellum du *Megaclinium falcatum*, in Mém. Acad. Roy. d. Sci. et Belles-lettres de Bruxelles, 1841.

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mentioned by Hooker[1], and described in more detail by Fitzgerald[2]; here the labellum is irritable to contact, a light touch at its free end causing the narrowed hinge hastily to contract, so that the labellum is raised and forms, together with the column and lateral petals, an almost closed box.

Hence it would appear that so far only two genuine cases of motile labellums have been recorded; *Megaclinium*, in which the movement is spontaneous, and *Pterostylis*, where it is called forth by an external stimulus. The object of the present paper is to give an account of the mechanism of movement of a new case, *Masdevallia muscosa*, Rchb. f.

Originally described by Reichenbach [3], from dried specimens collected in New Granada by Shuttleworth, it was only in May of this year (1887)—when a plant of it flowered in the Kew orchid-house—that the motility of the labellum of this species was discovered. This discovery is due to Mr. W. Bean, foreman of that house, and has been put on record in a recent number of the Gardeners' Chronicle[4]. Through the kindness of the Director of the Royal Gardens, and of Mr. Watson, I have been enabled to investigate this interesting phenomenon. I wish also to take this opportunity of acknowledging the help so freely rendered by Mr. Watson in connection with this and many other matters. The plant flowered a second time—five months later—so that I have been able to confirm and add to my earlier results.

Masdevallia muscosa produces a number of flowers borne singly on erect scapes some 15 cm. long. Figures 1 and 2, Pl. XII, show front and side views respectively of a single flower, slightly enlarged. The scapes are clothed with a dense covering of stiff glandular emergences—a most uncommon feature in *Masdevallia*. On the scape are inserted two sheathing scaly bracteoles (Fig. 2, br^1 and br^2), one about $\frac{1}{3}$ up, the other at the insertion of the flower. The ovary, covered with

[1] J. D. Hooker, Flora of Tasmania, vol. ii. p. 18.
[2] Fitzgerald, Australian Orchids, Sydney, 1882.
[3] Gard. Chron. Apr. 10, 1875.
[4] Gard. Chron. June 25, 1887.

shorter emergences, is at right angles to the scape. The sepals are triangular, and produced into long tails (see Figs. 1 and 2), yellow, with reddish nerves. The labellum—seen in the contracted position in Fig. 1, and in the expanded in Fig. 2—is roughly triangular and articulated by a delicate hinge to the foot. It possesses a median crest on its upper surface, on stimulating which the labellum is immediately drawn up into the flower. The two lateral petals, right and left of the column, are quite narrow, and their distal ends (*lp*) are seen projecting over the labellum in Fig. 1. The further details of the essential parts of the mechanism are given in full below. Reichenbach places the species in a group with *Masdevallia Echidna*, *M. Xipheres*, and *M. erinacea*.

Special Account of Labellum.

The labellum naturally falls into two segments. These are (1) a narrowed proximal flexible region, which I shall always refer to as the *neck* (*h* in Figs. 3, 4, 7, &c.), which is articulated to the foot, *ft.*,—a downward prolongation of the column; (2) a distal end-segment, triangular in form, the *blade* (*bl.* in Figs. 3, 4, &c.). The neck then is the region intermediate between the foot (from the insertion of the emergence *e*) and the blade.

The triangular blade has a slightly convex under-surface, marked by three low ridges (Fig. 5), which run mesially and right and left of the median plane respectively. Each ridge corresponds to a vascular bundle which runs in the subjacent tissue. These three bundles run continuously throughout the labellum, and are for the most part parallel, but towards the distal edge of the expanded blade they diverge considerably. On the upper surface of the blade is a most conspicuous median crest, commencing about 1 mm. from the distal end, and, after attaining a height of 1 mm., dying out in the region where the attenuated proximal corner of the blade passes into the neck. It is coloured a deeper yellow than the rest of the blade, due to the presence in its epidermis of very numerous yellow chromoplasts. Its broad distal part is coloured a deep

purple (shaded in the Figs.). As it passes into the neck the crest, *cr.*, gradually gives place to a shallow groove (seen in Figs. 6 and 11 d), which gradually dies out, and the neck—bent into a U-shape with the convexity downwards—is band-like with perfectly even upper surface (Figs. 3 and 11 e). At the point where the neck runs into the foot is inserted an emergence (*e*, Fig. 3) of an interesting nature. This emergence arises from the upper surface, and is about 1·5 mm. in length. It bridges over the concavity formed by the arching of the neck in the extended labellum (Fig. 3). Its tip is bent slightly upwards, and does not quite touch the point where neck and blade run into one another. Figure 6 shows the extended labellum looked at from above; it will be noticed that the neck, *h*, can be seen between the tip of the emergence and the groove at the proximal end of the blade. The foot, from the point of insertion of this emergence, gradually increases in thickness till it passes directly into the base of the column, with which it makes a slightly obtuse angle.

In Figure 11 I have represented diagrammatically a series of transverse sections of the labellum: a, b, c, &c. represent sections through the labellum at the points marked *a*, *b*, *c*, &c. in Fig. 12. In each the position and form of the vascular bundles are indicated. In every case the xylem is shaded, the phloem below it being outlined only. In the blade (Figs. 11 a, 11 b, and 11 c) in each of the three bundles the xylem is crescent-shaped, the horns of the crescent embracing, more or less, the phloem. The central bundle is drawn in Fig. 13 on a much larger scale. This section is taken from a point below the centre of the crest (corresponding to Fig. 11 c). The crescentic xylem consists of spiral tracheides, *tr.*, which are accompanied by a sheath of cells containing tannin to a marked degree. The extent of this tannin-containing sheath is indicated by the light flat wash carried over the cells (Fig. 13 *sh.*). All these cells have very large and conspicuous nuclei. Below the xylem is the small-celled phloem, *ph.*, of sieve-tubes, with horizontal and slightly callous sieve-plates, and companion-cells. As may be seen, the phloem is separated by a number

of layers of small prismatic cells from the xylem. These are only markedly tannin-containing within the limit indicated by the flat wash of colour. As the bundles pass from the blade to the neck, their elements undergo a most conspicuous flattening parallel to the upper and lower limiting surfaces of this part (cf. Figs. 11 d, 11 e, and 11 f). In Fig. 11 e is seen a section from the thinnest and most flexible part of the neck, where — as we shall see—the maximum amount of bending takes place. By this flattening the bundles come to lie in the neutral plane of curvature, and offer as little opposition as possible to bendings due to variations in the turgidity of the opposing sides. Quite the same sort of thing is found in the pulvinus of *Mimosa pudica*, and elsewhere. The elements of the three bundles in the neck are identical with those seen in Fig. 13. The bundles are however conspicuously flattened, occupying a much less vertical range than in the blade. It may be noted that it is here similarly accompanied by tannin-containing cells which have a wider distribution than in Fig. 13. They extend throughout the upper portion of the section, uniting the bundles, and extending upwards to the layer below the upper epidermis.

In the neck the ground-tissue consists of prismatic parenchymatous cells. That *below* the plane of the bundles is thick-walled, giving a rigidity to these parts of importance as will appear in the sequel. *Above* it consists of delicately thin-walled cells, with small intercellular spaces ; these thin-walled cells extend to the upper epidermis, and are probably the seat of contractility. The thick-walled cells of the lower half extend *between* the central and lateral bundles, but not beyond the level at which they run. The epidermis on either surface is thick-walled and but little cuticularised, that above quite plain ; but below, each epidermal cell is drawn out into a pointed papilla. The epidermis of the underside of the labellum is everywhere drawn out into larger or shorter sharp hairs, especially on the ridges over the bundles. The crest of the blade is formed entirely of thin-walled parenchyma with copious protoplasm. These cells show a well-defined continuity of protoplasm when treated with hydric sulphate and

Hoffmann's blue[1]. The fine uniting-strands show at the pit-closing membrane a swelling which, although I was unable to resolve it, no doubt represents a small spindle-like arrangement of very delicate filaments perforating the closing-membrane in a sieve-plate-like manner, and so uniting the strands from the respective cell-bodies (see Fig. 14). Gardiner[2] gives cases in which he met with a similar appearance due to the same cause. In the 'tannin-containing sheath' and in the neck a similar continuity exists.

The emergence, previously referred to, merits fuller notice. It is entirely non-vascular, originating simply as an outgrowth of the upper surface at the junction of foot and neck, and involves only the ground-tissue and epidermis. Fig. 11 g is a section of the foot *above* the point of insertion of the emergence, Fig. 11 f, just *below*. In Fig. 11 f transverse sections are given of both emergence (above), and neck (below), showing their relative position to one another. In Fig. 17 is seen a much-enlarged longitudinal section of the emergence with its upturned tip. The epidermis alone is fairly thick-walled, giving a certain elasticity to it, so that if the emergence be deflected downwards with a bristle, when the labellum is in the extended position, till it touches the neck, it will, on removing the deflecting force, immediately fly back to its former position.

Irritability and Movement.

The movement is displayed as a sudden and rapid folding up of the labellum on its band-like neck, so that the broad distal part of the blade is approximated to the top of the column (Fig. 4). The general view of the flower (Fig. 1) shows it with contracted labellum. This movement is called forth by the gentlest touch of a hair or insect's foot on the median crest of the blade. No other part of the blade is irritable in this way. Irritability is thus confined to the upper surface of the blade, and of this to some part of the

[1] Gardiner, On the Continuity of the Protoplasm, &c., in Phil. Trans. 1883, Part iii. p. 824.

[2] Loc. cit. p. 833; cf. Pl. 68, Fig. 5.

crest. Within a second of stimulating the crest the blade is moved upwards through an angle of some 10°, then for a brief space, which is only just appreciable and amounts to a small fraction of a second, a slight hesitation or slowing, as it were, is noticeable, and finally the upward movement is continued through a further angle of 70° or 80° with great rapidity. The whole process barely occupies two seconds[1]. In Fig. 4 the position of contraction is shown. By this act an almost entirely closed space is temporarily formed. The space is bounded posteriorly by the column, and anteriorly by the upfolded blade. The foot forms the floor, and three-fourths of the side parts are closed by the lateral sepals. The two lateral petals complete above the blocking of the sides (the position of one is represented in Fig. 4 by the dotted outline *l.p.*) and form a partial roof. Fig. 10 represents a flower looked down upon from above, the blade, *bl.*, being in the elevated position. The anther, *a*, is borne on the summit of the column of which the dorsal ribbed surface, *c*, is visible. The two pollen-masses project from the anther along the top of the rostellum (cf. Figs. 8, 9, and 10). The rostellum, *r.*, projects slightly into the space (*e*, Fig. 10) left between the two lateral petals, *l.p.*, which, considerably over-stepping the column, meet one another anteriorly. The distal surface of the blade, *bl.*, is seen drawn up and preventing any outlet between it and the two lateral petals.

A glance at Figs. 4 and 10 shows that the anther is *not* included in the closed space. From this it may be inferred that, should we have here a device for promoting cross-fertilization by insect-agency, it is no part of the plan that the insect captured should be confined within the flower till the labellum moves down again. Rather, on the other hand, is it essential that it should make its escape through the aperture described (*e*, Fig. 10), for this is the only means by which the pollinia can be removed. To this point I shall return.

[1] This account applies to flowers only for the first four or five days after opening. Subsequently, as they begin to pass off, the movement is more sluggish. Flowers will often last for fourteen days before withering.

Mechanism of movement.—From direct observation and experiment it seems that the cells concerned in this movement are confined to the upper half of the band-like neck. As in *Mimosa pudica* so here, in the contractile region there is a sudden loss of turgidity by the cells on that side towards which the movement occurs. We have here to deal with a case not common in the vegetable kingdom, and which finds its parallel in *Dionaea*. There is a complete differentiation between the parts which *receive* the stimulus, i.e. the crest of the blade, and the parts which *carry out* the movement, i.e. the neck. Further, the part where the contractile cells reside is in no way responsive to direct stimulus. Thus, if the upper surface of the neck be at any point touched gently with a hair or other body—such touch being amply sufficient to cause a contraction if applied to the crest direct—no contraction follows. In other plants there may be often a conduction of stimulus over some distance, but usually the part to which the stimulus is conducted is itself directly sensitive to external shock. Thus for instance in the stamens of *Sparmannia africana*, if any stamen be directly stimulated, it not only itself contracts, but also transmits the stimulus to other stamens, which likewise contract; so also in the stigmatic lobes of *Martynia*. In both these cases the part to which the stimulus is transmitted is also itself sensitive to an external stimulus. In *Dionaea*, however, a separation similar to that in our *Masdevallia* is found. In *Dionaea* sensitiveness to an ordinary touch is confined to the six tactile emergences on the upper surface of the leaf—three on each valve; the organ of movement (the hinge) is at some distance.

Fig. 3 shows the labellum in the extended position. On stimulating the crest the blade traverses an angle of some 10° slowly before developing the final rapid contraction. During the first period the blade is—so to speak—rounding the emergence. Any sudden contraction, with the parts as arranged in the figure, would result in the blade being jammed by the emergence. Such jamming occurs if the emergence be a trifle too high, as may be obtained by previous manipulation.

In order to avoid this, contraction is slow at first, beginning at the point where the blade runs into the neck, i. e. where the crest has given place to the groove. The blade is thus raised through a small angle, and the emergence satisfactorily circumvented (Fig. 7 a). The tip of the emergence now touches the groove, and would seem to be used as a sort of fulcrum, round which the blade continues its movement. The momentary check, recorded above, occurs at this period. There is now no hindrance to the completion of the movement, and the contraction has meanwhile extended further along the neck. The result is that the neck is raised slightly so as to be in contact with the under side of the emergence, the latter also being deflected a trifle downwards (from the pressure of the upfolding blade on its tip) to meet it. The final position is shown in Fig. 7 b; the emergence is now in contact with the proximal part of the crest above, and with the neck below.

Function of emergence.—The chief part played by the emergence is that of preventing the blade from overstepping its proper limit in contraction. Fig. 7 b shows how it is impossible for it to be approximated any nearer to the column. The emergence brings it to a dead stop.

If the emergence be removed by a transverse cut near its point of insertion (which can be effected from above with a sharp scalpel without injuring any other part of the flower), it is found that, on stimulation, the blade is often carried beyond its previous limit and tends to become jammed by the distal ends of the two lateral petals where they pass in front of the apex of the column. This overstepping and jamming is especially found to occur if the flower operated on be still young and the contraction rapid.

It may be that the emergence also assists the blade in its relaxation; for, being highly elastic (cf. page 242) and in the position of contraction somewhat diverted downwards, it will exert a certain continued pressure at the edge of the crest where it is in contact with it. I have, however, no

experimental evidence which would confirm this view—however, should it assist in this way, such a function is fortuitous and entirely secondary to that of limiting the angle covered in the movement.

I do not find in other Masdevallias anything corresponding to this emergence. It has no doubt been developed in connection with the special mechanism of contraction, which exists in this member of the genus only, so far as is yet known. In *Pterostylis*—a genus of Orchids far removed from *Masdevallia*—a quite analogous arrangement is, however, found. The labellum in this genus[1] is endowed with an irritability very much like that in *Masdevallia muscosa*. Figure 15 shows the relation to the column of the labellum both in the extended and in the contracted position (latter with dotted outline). In this connection I wish to call attention to the position of the emergence—*e'* and *e''* in the two positions respectively. There can I think be little doubt as to the emergence here preventing the labellum contracting beyond a certain limit; further contraction will cease when the emergence strikes against the foot. *ft*. This figure gives us the case of *P. Woolsii*, Fitzgerald, but in the majority of other species the emergence does not project downwards in such a rigid manner, but is thin, flexible and very usually fimbriated at its edge. Thus Fig. 16 represents *P. curta*, R. Brown, and in this case it would offer no such efficient opposition to the continued contraction of the labellum: and from Fitzgerald's figures and an examination of dry material I am by no means sure that it would press against the foot even if the labellum very considerably overstepped its normal limit. The speculation may be hazarded that in this genus there was at first developed—in connection with the motility—an emergence which limited the range of the labellum.

[1] The facts relating to *Pterostylis* are drawn from R. D. Fitzgerald's Australian Orchids, vol. i. Sydney, 1882. Mr. Fitzgerald gives a most interesting account of the part played in fertilization by the movement, and had been able to study the phenomena on the plants growing amid their natural surroundings. The two figures of *Pterostylis* (15 and 16) are schematised from his drawings.

This still retains its primitive function in *P. Woolsii* and in a few other species. In many species of *Pterostylis* it has become gradually modified for purposes of attraction by the appendaging and fimbriating it has undergone. In the relaxed position of the labellum this emergence occupies a prominent position in the mouth of the flower. That in this further adaptation the emergence has *entirely* lost its supposed primitive function I am unable to say; a few experiments on living material would easily enough decide[1]. In some species (*P. Woolsii*) the change of function has not occurred.

Though analogous in function, the emergence in these two genera has a quite different insertion. In *Masdevallia* it is inserted at the proximal end of the band-like neck, and is directed *forwards*; in *Pterostylis* at the distal end, and directed *backwards* (compare Figs. 4 and 16). Further, in the former it is entirely non-vascular, in the latter—in some cases, at any rate, from an inspection of dry material—it is supplied with a string of tracheides.

Transmission of stimulus.—As regards the nature of the change occurring in the cells which bring about the contraction, i. e. those of the upper side of the neck, there seems no reason that it should differ from that in the contractile half of a pulvinus of *Mimosa*. It will be remembered that in this case the stimulus causes a loss in turgidity of the cells of one-half, so that these no longer offer any antagonism to the still turgid cells of the other half: hence the movement. As in the pulvinus of *Mimosa*, so in *Masdevallia*, numerous small intercellular spaces are present between the corners of the thin-walled cells of the upper half of the neck, and the phenomenon of contraction is no doubt due to a sudden diminution of turgidity in this part, accompanied by an outflow of water into the intercellular spaces. Whether there be a definite act of contraction by the protoplasm which causes an out-passage of water by filtration under pressure (Vines), or whether there be a sudden diminution of osmoti-

[1] Fitzgerald gives no observations as to the function of the emergence. For the suggestions here made I am alone responsible.

cally active substances (Pfeffer), is a question which I think would be unsuitable for discussion here, involving as it does physiological principles of fundamental importance. The extended condition is arrived at by the gradual re-absorption by these cells of water, the former equilibrium between the two halves being re-inaugurated. In *Masdevallia* this occurs some twenty minutes after contraction; the act of descent of the blade not occupying more than five minutes when once it has commenced.

I made an extremely delicate cut across the upper surface of the neck, at a point nearer the blade than the emergence, severing the epidermis and subjacent layers, but leaving the bundles intact, and the labellum in the single case thus operated on remained in the contracted position for many hours and finally moved down only through about 10°, and in this position remained until the fading of the flower. This experiment is the counterpart of cutting through the contractile half of a pulvinus of *Mimosa*, and has a result quite similar.

It remains for me to describe certain experiments undertaken to ascertain the course followed by the stimulus.

(1) A clear transverse cut was made across the crest of the blade (Fig. 18, A) separating it into a proximal and distal portion. Care was taken that this cut should not reach the plane of the vascular bundles. When the labellum had assumed the extended position the crest was stimulated with a hair, in the ordinary way, on the *distal* side of the cut (at X, Fig. 18). A normal contraction immediately occurred, the cut not impeding the course of the stimulus.

(2) The cut was then continued further down, so as to sever the three vascular bundles. On stimulating again at X no contraction took place. If, however, the crest was stimulated on the *proximal* side of the cut an ordinary contraction resulted.

These two experiments point to the fact that the stimulus —initiated at the surface of the crest—passes, not along the surface or subjacent tissue to the contractile cells of the neck,

but rather vertically downwards to the neighbourhood of the vascular bundles and then travels in or near them to the neck. In the second experiment, in which the bundles were cut, no stimulus was transmitted.

(3) A further experiment was made on another flower. A transverse cut across the blade was made from below (Fig. 18, B) so as to sever the vascular bundles; the cut was not continued upwards and the crest remained intact. On stimulating the crest at a point on the distal side of the cut it was found that a contraction occurred only after repeating the stimulus and then was somewhat sluggish. The stimulus here had to travel obliquely downwards and forwards to reach the uncut part of the vascular bundles; the slowness of the transmission here being perhaps due to the unaccustomed oblique route to be traversed in reaching the bundle, whilst normally the stimulus would make its way directly to the vascular bundles, i. e. vertically downwards, and be rapidly transmitted to the contractile region.

In Fig. 13 the xylem is seen to be accompanied by a conspicuous sheath of thin-walled parenchyma with copious tannin content (see p. 241). It seems to me quite possible that the stimulus travels by this sheath, although I know very well that the experiments above recorded do not show whether the stimulus travels by this sheath or by some other element of the bundle. All they indicate is that it passes in the immediate vicinity of the bundle, not necessarily as a wave of disturbance in the tracheides. In a former paper [1] I have tried to show for the case of the stigmas of *Martynia*, and others, that it is *not* the string of tracheides which conducts the stimulus, but the general parenchyma. In the case of *Masdevallia*, I believe the parenchyma, which conducts the stimulus, to be consolidated with the vascular bundle, constituting the tannin-containing sheath referred to. In *Martynia* we have to deal with a more generalised case, the vascular and stimulus-conducting tissues not being approximated. The conducting

[1] F. W. Oliver, Ueber Fortleitung d. Reizes bei reizbaren Narben, in Ber. d. deut. bot. Ges. 1887, p. 162.

parenchyma in the stigma of *Martynia* is diffused, in *Masdevallia muscosa* concentrated; in relation to this it must be remembered that in the former the movement is a slow one, but in the latter very rapid; indeed we have to deal with a highly specialised mechanism in this case. A parallel case is found in the concomitancy of nerves and blood-vessels in a highly developed animal.

The presence of so much tannin in the cells of the supposed conducting sheath would tend to point it out, other things being equal, as a stimulus-conducting tissue. Gardiner[1] has shown that the amount of tannin present in a motile organ is often proportional to its irritability.

The conduction is probably facilitated by the 'continuity of protoplasm' which may be demonstrated in these parts. I have shown it for the parenchyma of the crest (Fig. 14), and also for the conducting sheath.

Biological Significance.

This manifestation of movement in the labellum seems to be simply one of the numerous ways chanced on by orchids in promoting cross-fertilization by the agency of insects. A small fly alighting on the extended labellum is immediately enclosed as it were in a box, and the only mode of exit is at the top, the aperture being bounded laterally by the two lateral petals, and posteriorly by the rostellum (Fig. 10). The insect will have to climb up the face of the column (Fig. 8), and in passing through the aperture the pollinia will be removed, the mucilage from the end of the rostellum sticking them firmly to the insect. It would be almost impossible for the insect to escape without removing them. I have often imitated this action with a blunt needle, passing its end through the aperture. The pollinia were always brought away with it.

For the completion of the act of cross-fertilization, it must be supposed that the insect next visits another flower, and

[1] Gardiner, On Tannins in Vegetable Cells, in Proc. Camb. Phil. Soc. vol. iv. p. 391.

being similarly entrapped, leaves the pollinia sticking to the viscid stigmatic surface, up which it has to crawl in making its escape. I have often caused small house-flies and ants to become thus entrapped; but unfortunately they did not make their escape, but after struggling awhile became quiescent. This of course is one of the disadvantages attendant on biological experiment made on plants removed from their natural surroundings.

In *Pterostylis* the part played by the mechanism is similar. Fitzgerald [1] has shown that in this genus small insects alight on the labellum, and, from its irritability, become enclosed within the flower. He has been fortunate enough to observe the removal of the pollinia by their agency. In *Pterostylis*, as in *Masdevallia*, the one way of escape is by crawling up the column and past the rostellum. The upper part of the column is provided with wings which bound the passage, just as the lateral petals do in *Masdevallia*. Fertilization is due, he says, chiefly to small dipterous insects.

As in *Pterostylis* the labellum is sensitive equally on upper and under surfaces, the insects very often fail to be entrapped, the labellum closing from any casual contact they may make with its under surface. This will be especially the case in those species in which the labellum is partly enclosed in the flower, and from its position very liable to be touched on the wrong side.

In *Masdevallia muscosa* the irritability is limited to the crest on the upper surface of the blade, and, so far as can be judged, it appears to possess altogether a more highly specialized mechanism. In either case it is not obvious that the possession of irritability is a very advantageous mechanism for securing cross-fertilization. Many other orchid-mechanisms will, I think, compare favourably with it for efficiency, since the disturbance caused by even a gentle breeze is quite sufficient to bring about the closing of the flowers, which will not open again for from twenty minutes to an hour.

As to the very numerous emergences present on the

[1] Fitzgerald, Australian Orchids, vol. i. Sydney, 1882.

flower-stalks (Figs. 1 and 2), these keep off undesired insects which might otherwise interfere with the mechanism. I have often watched ants trying to climb up, but they never got beyond the first bracteole (br^1). The emergences are of course discontinuous at this point, and the ant finding them beginning again usually desists.

I have not yet mentioned that at night the labellum assumes a position of 'sleep,' identical with that of contraction. I have repeatedly found that labellums which were 'down' at dusk were 'up' by 10 p.m., though I have never had the good fortune to find them in a partially closed condition. The sleeping here may be to protect the delicate mechanism from hurt by nocturnal radiation.

On one occasion the plant was placed during the day-time for several hours (from 11 a.m—3 p.m.) in a dark chamber. The labellums remained, however, in the extended position throughout the whole time.

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EXPLANATION OF FIGURES IN PLATE XII.

Illustrating Mr. F. W. Oliver's paper on the Sensitive Labellum of *Masdevallia muscosa*, Rchb. f.

Figs. 1 and 2. Front and side views respectively of a flower of *Masdevallia muscosa*. *a*. anther. br^1. lower bract. br^2. upper bract. *l*. labellum. *l.p.* lateral petal. *l.s.* lateral sepal. *p.s.* posterior sepal. In Fig. 2 the labellum is extended, in Fig. 1 contracted. Slightly larger than life.

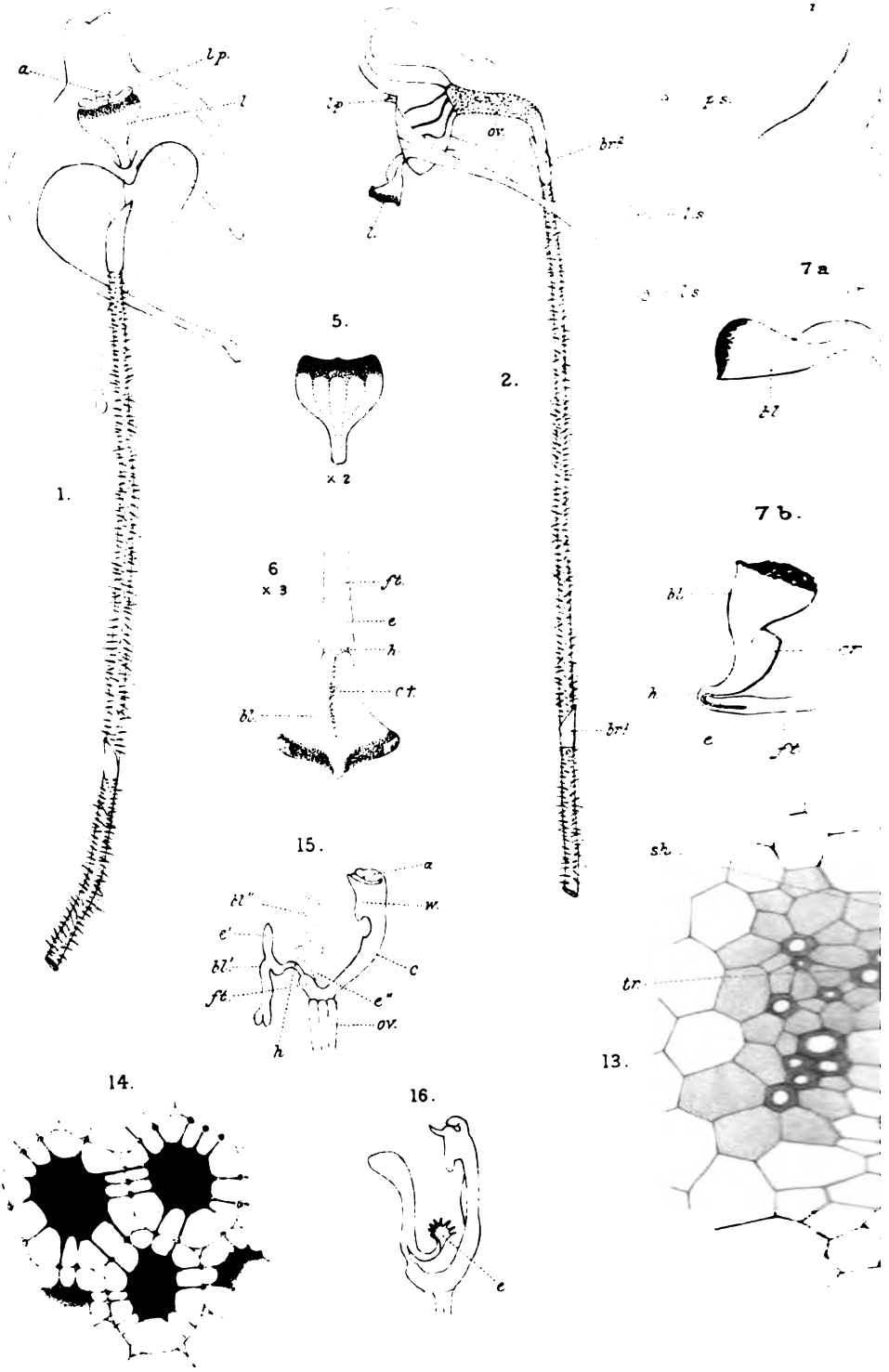
Fig. 3. Diagrammatic side view of column and extended labellum, the other parts of the flower being removed. *a* anther. *bl.* blade of labellum. *c* column. *cr.* crest. *e* emergence. *ft.* foot. *h* neck. *r.* rostellum.

Fig. 4. Diagrammatic side view of column and contracted labellum. Position of lateral petals indicated at *l.p.* Other lettering as in Fig. 3.

Fig. 5. View of under surface of blade. + 2.

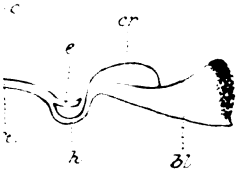
Fig. 6. Foot and labellum seen from above. *bl.* blade. *cr.* crest. *e* upper surface of emergence. *ft.* foot. *h* neck seen between emergence and blade.

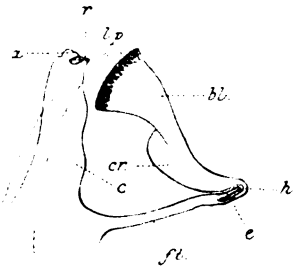
Fig. 7a. Position of blade after moving through about angle of 10°, to show the rounding of the emergence.

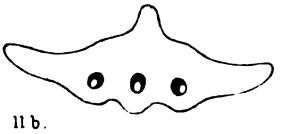


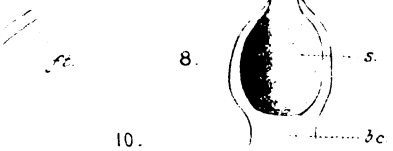
F. W. Oliver del.

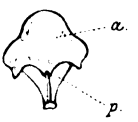
OLIVER.— ON THE LABELLUM IN MASDEVALLIA MUSCOSA, Rchb

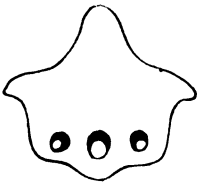


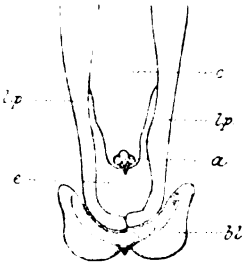


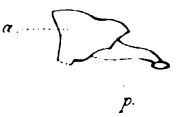


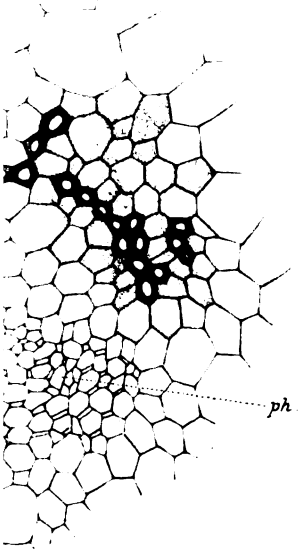


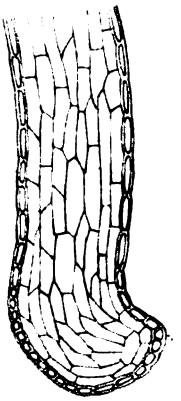












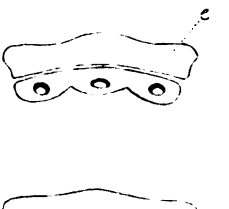


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Fig. 7b. Labellum in position of contraction.

Fig. 8. Front view of column. *a* anther. *b.c.* base of column. *r.* rostellum. *s.* stigmatic surface.

Figs. 9a and 9b. Views from side and above of anther *a*. *p.* pollinia.

Fig. 10. Diagrammatic view of flower from above. *a* anther. *c* dorsal side of column. *e* aperture by which the insect escapes. *b.l.* labellum. *l.p.* lateral petal. Labellum is in position of contraction.

Fig. 11. Series of diagrammatic transverse sections corresponding to dotted lines *a*, *b*, *c*, &c. in Fig. 12. 11a. through distal part of blade; 11b. through beginning of crest; 11c. through middle of crest; 11d. through region where blade passes into neck; 11e. through the neck at point of bending; 11f. through the neck below point where emergence is given off; shows the emergence, *e*, in its natural relation to the neck; 11g. through foot just above insertion of emergence.

Fig. 12. Key to Fig. 11, showing points at which a, b, c, &c. have been taken.

Fig. 13. Transverse section through the central vascular bundle from Fig. 11c. *ph.* phloem. *sh.* tannin-containing sheath. *tr.* tracheides.

Fig. 14. Shows continuity of protoplasm from a transverse section of the crest treated with hydric sulphate and Hoffmann's blue.

Fig. 15. *Pterostylis Woolsii*. Lateral view of column and labellum, showing relative positions in the extended and contracted state. The labellum is dotted in the latter. *a* anther. *bl'*. *bl''*. blade of labellum in extended and contracted states respectively. *c* column. *e*. *e'*. emergence in the two positions. *ft.* foot. *h.* neck of labellum. *ov.* ovary. *w.* wing of upper part of column (after Fitzgerald).

Fig. 16. *Pterostylis curta*. Similar view showing fimbriated emergence *e*. The labellum is in the contracted state (after Fitzgerald).

Fig. 17. Longitudinal section through the emergence of *Masdevallia muscosa*.

Fig. 18. Diagram illustrating nature of experiments made. A, position of cut in experiment 1, afterwards continued through the vascular bundles (dotted line). B, cut in experiment 3, cutting the bundles from below. X, point stimulated.

The Effect of Cross-Fertilization on Inconspicuous Flowers.

BY

ANNA BATESON,

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IN discussing the relation of the conspicuousness of flowers and the advantages of cross-fertilization, Darwin comes to the conclusion that small inconspicuous flowers, which are not visited by insects as a rule, and which are perfectly self-fertile, must probably still be capable of benefitting by an occasional cross, for if they could not benefit in this way their flowers would gradually have become cleistogene. 'As therefore no species which at one time bore small and inconspicuous flowers has had all its flowers rendered cleistogene, I must believe that plants now bearing small and inconspicuous flowers profit by their still remaining open, so as to be occasionally intercrossed by insects. It has been one of the greatest oversights in my work that I did not experimentise on such flowers, owing to the difficulty of fertilising them, and to my not having seen the importance of the subject[1].' The following experiments were undertaken in the hope of deciding this question. The plants experimented on were *Senecio vulgaris*, *Capsella Bursa-pastoris*, and *Stellaria media*.

I.—SENECIO VULGARIS.

With regard to this plant, H. Müller says that the nectar is easily accessible in the tubular florets, but the absence of ray-florets and the small diameter of the capitula render them very inconspicuous, and he never saw them visited by insects[2]. This plant is perfectly adapted for self-fertilization,

[1] Darwin, Cross and Self-Fertilization of Plants, p. 387.

[2] H. Müller, Befruchtung der Blumen, p. 399.

[Annals of Botany, Vol. I. Nos. III and IV. February 1888.]

as the pollen is ripe by the time the stigma pierces the ring of anthers. The plants used in my experiments were obtained from the same locality when still young, and were grown in pots. Two capitula on one of the plants were cross-fertilized when most of the stigmas were extended, by rubbing over them a capitulum of another plant which was covered with ripe pollen. This method of crossing is very rough, but the crossing of all the florets would not be any better ensured by attempting to cross each one individually. The plant from which pollen was taken for crossing was a weaker plant than the one with which it was crossed. Two capitula on the same plant were marked for self-fertilization, and these were allowed to fertilize themselves, and were not artificially self-fertilized. This plant was not covered by a net, though it would have been better to have been so. When ripe the capitula were gathered, and there was found to be a considerable difference in the fecundity of the cross and self-fertilized capitula. The two self-fertilized capitula contained between them 69 seeds and 42 sterile ovules; whilst the two cross-fertilized capitula contained between them 125 seeds and only 8 abortive ovules.

The seeds from the two lots were allowed to germinate, and the seedlings were planted out in pairs on the opposite sides of pots, which were so placed as to have the plants of the two sides exposed equally well to light. The self-fertilized seeds germinated slightly before the cross-fertilized ones. When full-grown the plants of both sides were measured, and the result is shown in the table opposite.

The figures in columns D, E, and F show that with only three exceptions the crossed exceeded the self-fertilized plants in height, besides which the tallest crossed plants were decidedly higher than the tallest self-fertilized ones. The total height of all the crossed is to the total height of all the self-fertilized plants as 100 to 87. When weighed the two lots showed hardly any difference, the weight of the crossed plants being 108·7 grms., and the weight of the self-fertilized 105·5 grms., or as 100 to 97. In fecundity the crossed plants showed an advantage over the self-fertilized, the average

number of seeds per capitulum of the cross-fertilized being to the average number per capitulum of the self-fertilized as 100 to 73.

TABLE I.—SENECIO VULGARIS.

In their original order.			In order of magnitude in a single series.		
A	B	C	D	E	F
	Crossed.	Self-fert.	Crossed.	Self-fert.	Difference.
	cms.	cms.	cms.	cms.	cms.
Pot I	10·4	8·0	19·5	15·0	−4·5
	13·4	12·5	19·0	13·9	−5·1
	10·0	12·7	17·5	13·7	−3·8
Pot II	10·5	9·5	14·4	12·8	− 1·6
	13·2	15·0	13·4	12·7	− 0·7
Pot III	11·6	12·8	13·2	12·5	−0·7
	12·0	12·0	12·0	12·0	±0
	14·4	11·6	11·6	12·0	+0·4
Pot IV	19·0	13·9	11·5	11·6	+0·1
	10·5	9·0	10·7	9·9	−0·8
Pot V	10·5	8·5	10·5	9·5	−1·0
Pot VI	10·7	8·8	10·5	9·0	− 1·5
Pot VII	11·5	13·7	10·5	8·8	−1·7
	19·5	9·9	10·4	8·5	−1·9
	17·5	12·0	10·0	8·0	−2·0
Total in cms.	194·7	169·9			

II.—CAPSELLA BURSA-PASTORIS.

According to H. Müller, this species is visited by insects to some extent, but its flowers are very inconspicuous and perfectly self-fertile[1]. The plants used were taken from the same

[1] Befruchtung d. Blumen, p. 138.

locality when young and grown in pots. One of them was netted, and several flowers on it were cross-fertilized as soon as they were open with pollen from one of the other plants. The flowers are not easy to cross, as they are very minute, and the petals are nearly closed over the stigma. Flowers of the same age as the crossed ones were marked for self-fertilization. The seeds of the two lots germinated simul-

TABLE II.—CAPSELLA BURSA-PASTORIS.

In their original order.			In order of magnitude in a single series.		
A	B	C	D	E	F
	Crossed	Self-fert.	Crossed	Self-fert.	Difference
	inches.	inches.	inches.	inches.	inches.
Pot I	$14\frac{1}{8}$	$8\frac{4}{8}$	$15\frac{3}{8}$	18	$+2\frac{5}{8}$
Pot II	$15\frac{3}{8}$	16	$15\frac{1}{8}$	$16\frac{4}{8}$	$+1\frac{3}{8}$
	13	$16\frac{4}{8}$	$14\frac{7}{8}$	16	$+1\frac{1}{8}$
Pot III	$14\frac{3}{8}$	$14\frac{4}{8}$	$14\frac{3}{8}$	$14\frac{4}{8}$	$+\frac{1}{8}$
Pot IV	$15\frac{1}{8}$	$9\frac{7}{8}$	$14\frac{1}{8}$	$13\frac{5}{8}$	$-\frac{4}{8}$
	$14\frac{7}{8}$	18	$13\frac{6}{8}$	13	$-\frac{6}{8}$
Pot V	$13\frac{1}{8}$	13	$13\frac{1}{8}$	$12\frac{2}{8}$	$-\frac{7}{8}$
	$13\frac{6}{8}$	$13\frac{5}{8}$	13	$9\frac{7}{8}$	$-3\frac{1}{8}$
	$12\frac{4}{8}$	$12\frac{2}{8}$	$12\frac{4}{8}$	$8\frac{4}{8}$	-4
Total in inches.	$126\frac{2}{8}$	$122\frac{2}{8}$			

taneously, and were planted out on the opposite sides of pots. The self-fertilized plants exceeded the crossed in height at first; but at the last measurement the crossed slightly exceeded the self-fertilized plants in total height. The relation of crossed to self-fertilized plants shown in the totals on the table is as 100 to 96, so that there cannot be said to be more than a very trifling difference in height. By weight, however,

the crossed showed a decided advantage over the self-fertilized, being as 100 to 88.

III.—STELLARIA MEDIA.

This plant appears to be not invariably self-fertilized, as it is occasionally visited by insects for its nectar. But as it flowers through the winter as well as in summer, it must, in the absence of insects, depend on self-fertilization; besides which, it is very inconspicuous, except when growing luxuriantly in large masses. Some young plants of *Stellaria* were growing in a flower-pot in a greenhouse, and these were planted in separate pots. One of them was netted, and some of its flowers were crossed with pollen from one of the other plants after their own stamens had been removed whilst still unripe. Other flowers on this plant were marked at the same time for self-fertilization, and allowed to fertilize themselves. In this case the capsules of the cross-fertilized flowers were found to contain rather fewer seeds than those of the self-fertilized ones, the average number in the former capsules being eight, and in the latter ten. The seedlings from the two lots were planted on the opposite sides of seed-pans, and were first measured when in a very young stage before the stems had become decumbent. The fifteen crossed seedlings measured $16\frac{5}{16}$ inches, and the fifteen self-fertilized $15\frac{2}{16}$, but the four tallest crossed were to the four tallest self-fertilized as 100 to 81. When full-grown the longest branch of each was measured, with the result as in Table III (see p. 260).

Columns D, E, F of Table III show that in nearly every case the crossed plants slightly exceed the self-fertilized in length, although the total only gives a relation of 100 to 95. However, in a procumbent and much branched plant of this kind, a comparison of the lengths of the longest branch in each pair is not a very good test; for, whenever the longest branch of the one exceeds the longest branch of the other, the shorter branches of the stronger plant would probably also exceed the shorter branches of the weaker plant. By weight, which is a better test in a case of this kind, the cross-fertilized were

to the self-fertilized as 100 to 91. It may be of interest to mention that these plants were crossed very early in the year, between February 14 and March 1, which is rather earlier than the season at which they have the best chance of being crossed in a state of nature [1].

TABLE III.—STELLARIA MEDIA.

Original order.			Single series.		
A	B	C	D	E	F
	Crossed.	Self-fert.	Crossed.	Self-fert.	Difference.
	inches.	inches.	inches.	inches.	inches.
Pot I	$8\frac{4}{8}$	$7\frac{6}{8}$	$8\frac{6}{8}$	$9\frac{2}{8}$	$+\frac{4}{8}$
	$8\frac{5}{8}$	$7\frac{1}{8}$	$8\frac{5}{8}$	$8\frac{5}{8}$	± 0
	8	$7\frac{1}{8}$	$8\frac{4}{8}$	$8\frac{5}{8}$	$+\frac{1}{8}$
Pot II	6	6	$8\frac{2}{8}$	$8\frac{3}{8}$	$+\frac{1}{8}$
	$7\frac{5}{8}$	$8\frac{5}{8}$	$8\frac{2}{8}$	$7\frac{6}{8}$	$-\frac{4}{8}$
	$8\frac{6}{8}$	$8\frac{5}{8}$	8	$7\frac{5}{8}$	$-\frac{3}{8}$
Pot III	$8\frac{2}{8}$	$9\frac{2}{8}$	$7\frac{5}{8}$	$7\frac{4}{8}$	$-\frac{1}{8}$
	$7\frac{5}{8}$	$8\frac{2}{8}$	$7\frac{5}{8}$	$7\frac{1}{8}$	$-\frac{4}{8}$
	$8\frac{2}{8}$	$7\frac{5}{8}$	$7\frac{4}{8}$	$7\frac{1}{8}$	$-\frac{3}{8}$
Pot IV	$7\frac{4}{8}$	$6\frac{5}{8}$	$7\frac{3}{8}$	7	$-\frac{3}{8}$
	$7\frac{2}{8}$	$5\frac{2}{8}$	$7\frac{2}{8}$	$6\frac{5}{8}$	$-\frac{5}{8}$
	$7\frac{3}{8}$	$5\frac{4}{8}$	$6\frac{6}{8}$	6	$-\frac{6}{8}$
Pot V	$6\frac{3}{8}$	$7\frac{4}{8}$	$6\frac{3}{8}$	$5\frac{6}{8}$	$-\frac{5}{8}$
	$6\frac{6}{8}$	$5\frac{6}{8}$	6	$5\frac{4}{8}$	$-\frac{4}{8}$
	6	7	6	$5\frac{2}{8}$	$-\frac{6}{8}$
Total in inches.	$112\frac{7}{8}$	$108\frac{1}{8}$			

Of the three species used for experiments *Senecio vulgaris* shows a greater advantage from cross-fertilization than either of the others; this advantage being not inferior to that ascertained for an average conspicuous and insect-fertilized plant.

[1] H. Müller, Befruchtung, p. 183.

The relation of the crossed to the self-fertilized plants is given as 100 to 86 in the cases of *Iberis umbellata*, *Origanum vulgare*, and *Lupinus pilosus*; 100 to 88 for *Ononis minutissima*, and 100 to 89 for *Papaver vagum*[1]. In the cases of *Stellaria media* and *Capsella Bursa-pastoris*, the cross-fertilized show an undoubted advantage over the self-fertilized, when both weight and size are considered, although the advantage in size alone is not so considerable. And it should be remembered that in such a case as *Capsella* cross-fertilization is very difficult to effect without injury to the flower, so that the seeds of self-fertilized flowers obtained by natural fertilization may have had an advantage to start with over those of the crossed ones. In the case of *Polygonum aviculare*, which is still more difficult to cross-fertilize, I have noticed that the seeds of crossed flowers look poor and deformed; and among some capsules of artificially self-fertilized seed of *Capsella*, obtained since the experiment given above, one of the capsules was deformed. Thus it would have been a better method to have obtained the self-fertilized seeds by artificial fertilization also. If, however, the relations of the crossed to the self-fertilized plants given above be taken as true, they would show that inconspicuous flowers do benefit by a cross, though apparently in a less degree than those adapted for cross-fertilization.

In conclusion, I should wish to thank Mr. F. Darwin for the very kind assistance which he has given me in this work.

[1] Darwin, Cross and Self-Fertilization, chap. vii. Table A.

BOTANICAL LABORATORY, CAMBRIDGE.

Microscopical Anatomy of the Common Cedar-Apple (Gymnosporangium Macropus).[1]

BY

ELMER SANFORD.

With Plate XIII.

THIS species of cedar-apple originates in the leaves of the smaller branches of *Juniperus virginiana*. The mycelium of the fungus causes an abnormal growth in the leaf tissue, which carries up the apex of the leaf as it develops, and pushes the branch to one side until the knot itself appears to be terminal. The growth thus produced varies from about a twelfth of an inch to an inch and a half in diameter, and finally becomes reniform from the cells of the outer part of the knot multiplying more rapidly than those at the base. The knots are of a silvery-gray colour. About the first of May, after the knots have remained over winter, the mycelium of the fungus collects in masses a little beneath the surface, raising it up into little papillae, varying in number according to the size of the knot, but usually appearing over the surface about an eighth of an inch apart. Later, the surface of the knot is broken through at these points, and yellow cylindrical masses, composed of spores borne upon long hyaline and more or less gelatinous stalks, are protruded, and, when moist, swell up, and often extend to the length of nearly an inch. Figure 1 is a drawing of one of these cedar-apples as it appeared the twelfth of May; *a* the branch on which it is borne, *b* the body of the apple, *c* one of the spore-masses, and *d* the ring at the base of the spore-

[1] This study was carried on in the Botanical Laboratory of the University of Michigan in May and June, 1887, under the direction of Professor V. M. Spalding.

[Annals of Botany, Vol. I. Nos. III and IV. February 1888.]

mass. By about the first of June these spores have fully matured, and the spore-masses begin to dry up and decay, afterwards falling off from the knot, which also dies and dries up, but much more slowly.

The foregoing general description, based on my own observations, agrees substantially with that given by Dr. Farlow in the 'Gymnosporangia or Cedar-Apples of the United States.' The following study of the anatomy of the knot was made independently, and so far as I am aware the results have not been recorded elsewhere.

That we may more fully understand the changes which take place, resulting in the production of the cedar-apple above described, it will be necessary first to notice the structure of the normal leaf.

A cross section of the leaf of *Juniperus virginiana* shows, passing from the periphery towards the centre, (1) a distinct epidermal system, (2) a layer of rather large parenchymatous cells, making up the greater part of the leaf, and (3), near the centre, the fibrovascular bundle. The epidermal system varies somewhat on the inner and outer surfaces of the leaf. On the outer surface is a distinct and quite thick cuticle, and beneath this usually about two layers of quite regular epidermal cells covering the parenchymatous cells. The epidermis of the inner surface of the leaf consists of one layer of rather large epidermal cells of a more spherical outline. Here there are many stomata.

The parenchymatous tissue is made up of rather large ellipsoidal cells loosely packed together, with many intercellular spaces, and with very definite and somewhat thick cellulose walls, in which are often thin places. The cells of the parenchymatous tissue, at the time of observation, were quite full of starch.

The vascular bundle is of the collateral type, the xylem lying on the side towards the inner surface of the leaf, and the phloem towards the outer. The xylem is composed of scalariform and reticulated tracheids.

Turning now to the structure of the cedar-apple, we find

it composed of the same tissues that go to make up the substance of the normal leaf, but all of them modified, the differences being specially marked in the epidermal system.

The vascular system enters the knot as one bundle given off from the vascular bundle of the branch of the tree. At first it is doubtless a simple bundle of the collateral type, but as the knot increases in size the vascular bundle developes rapidly until it soon appears like the vascular system of a branch—a number of collateral bundles placed side by side, thus forming a complete zone at the centre of a cross section. Soon after entering the base of the knot the vascular bundle divides into a number of branches which radiate in all directions throughout the substance of the knot, and which in turn give off small radiating branches. Fig. 2, which is a diagram of a longitudinal section of one of these knots, shows, *a*, the location and manner of branching of the vascular bundle. A cross section of one of these small bundles, such as would be found at *a'*, appears as a nearly circular mass of somewhat irregular cells surrounded by larger, more nearly circular, parenchymatous cells. Comparing this with the cross section of the bundle of a normal leaf, there is found a strong resemblance, but the elements of the bundle of the knot are enlarged, show a marked indication of distortion, and there is little distinction between xylem and phloem. The larger part of the vascular bundle of the knot is composed of scalariform and reticulated tracheids.

Much the larger part of the knot is formed by somewhat elongated, parenchymatous cells, closely resembling those of the normal leaf, but much larger, with thicker walls, and the cells themselves rather more loosely packed together, leaving very many and quite large intercellular spaces. The position and relative extent of this tissue is shown in the diagram, Fig. 2, *b*. Commonly each cell appears as if it had a distinct wall of its own, so that between two adjacent cells the wall is double, but sometimes these walls have the appearance of having fused together, and often at these places

will be found a thin spot in the wall. Fig. 4 shows a number of these cells in longitudinal section; and Fig. 3, *b*, shows others as they appear in section just beneath the epidermis of the knot.

The epidermis, as before stated, bears little resemblance to that of the normal leaf. It consists of a layer of corky cells, about four cells in thickness, and covered externally by what appears to be the flattened and shrivelled-up remains of similar cells, forming a thin layer over the surface. These cork-cells are shown in cross section in Fig. 3, *a*. It is the epidermal tissue that is raised up and broken through by the spore-masses, Fig. 1, *c*; and it is this tissue, together with the thick masses of mycelium that collect beneath it at these points, which form the rings at the bases of the spore-masses, Fig. 1, *d*.

The mycelium of the fungus penetrates to the interspaces between the parenchymatous cells of the leaf, and developing there in great abundance, in some way stimulates the tissues to this abnormal growth, Fig. 4. The mycelium is rather coarse, contains many yellow oil-globules, has very definite cell-walls, and branches very frequently. It is a continuous tube without septa, save at the places where it collects to form the spore-masses, Fig. 2, *c*. The fungus draws nourishment from the cells of the knot by means of rather large haustoria which penetrate through the walls and develop within the cells; their contents are very granular, and their walls are not so firm and definite as are the walls of the mycelium, Fig. 5. At the bases of the spore-masses the mycelium forms even more of the substance of the knot than do the cells of the host, which are here quite small, with often very indefinite cell-walls, and themselves appear to be completely isolated from one another by the mycelium which surrounds them. Fig. 6 is a section through one of these places, *a* the line along which the spore-mass was attached (corresponding to *c* in Fig. 2), *b* some epidermal cells of the knot lying at the edge of the opening made by the protruding mass, and *c* the parenchymatous cells of the host. At these

places the walls of the closely packed and interwoven mycelial filaments often fuse one with another, and, the adjacent parts becoming absorbed, form a pseudo-parenchyma. From these dense collections of mycelium long hyaline filaments are given off, and, together with the spores which they bear upon their outer ends, form the spore-masses, Fig. 1, *c*. The greater portion of the central part of these masses is composed of spore-bearing filaments, and the spores are mostly at or near the surface of the masses. The spore-bearing filaments form the so-called 'gelatinous' part of the spore-mass. Each filament is a tube whose lumen has become nearly obliterated by the thickening of the walls. When placed in water the walls of these filaments swell rapidly, both in length and thickness, and their walls adhere together until they all appear to form a solid, almost homogeneous mass; but if this mass be then treated with absolute alcohol, it is shrunken until the individual filaments stand out distinctly, as shown in Fig. 8. These facts are easily demonstrated by cutting longitudinal sections of spore-masses and treating alternately with water and alcohol while watching them under the microscope.

The spores are two-celled and their contents are very granular. Their walls are thick and definite, as is commonly the case with the walls of teleuto-spores, Fig. 7.

All drawings, except figures 1 and 2, were made with a camera. In this investigation I found the use of reagents generally of little assistance, but derived better results from material gathered and preserved in alcohol than from fresh material used.

Summarizing briefly the changes which take place in the leaf as the result of the attack of the fungus:

1. The most striking is the great multiplication of cells, and their generally enlarged size.

2. The cell-walls are thicker, and their deportment towards reagents is much more like that of the fungus-filaments than that of the cells of the normal leaf.

3. The fibrovascular system is developed until it assumes

equal importance with that of a branch, and it divides in a peculiar radiating manner throughout the knot, while the elements of the bundle are more distorted and less-regularly placed.

4. The epidermal system of the leaf has entirely disappeared, its place being taken by a few layers of cork-cells, covered over by the thin layer of cells, dead and shrivelled, as already described.

EXPLANATION OF FIGURES IN PLATE.

Illustrating Mr. Elmer Sanford's paper on the Anatomy of the Common Cedar-Apple (*Gymnosporangium Macropus*).

Fig. 1. One of the knots, natural size. *a*, The stem on which it is borne. *b*, The body of the knot. *c*, One of the spore-masses. *d*, Ring at the base of the spore-mass.

Fig. 2. Diagram of a longitudinal section of a knot. *a*, The vascular bundle. *b*, Parenchyma of the knot. *c*, The mass of fungus-filaments at the place from which the spore-mass arises.

Fig. 3. *a*, Corky epidermal system of the knot. *b*, Parenchyma beneath.

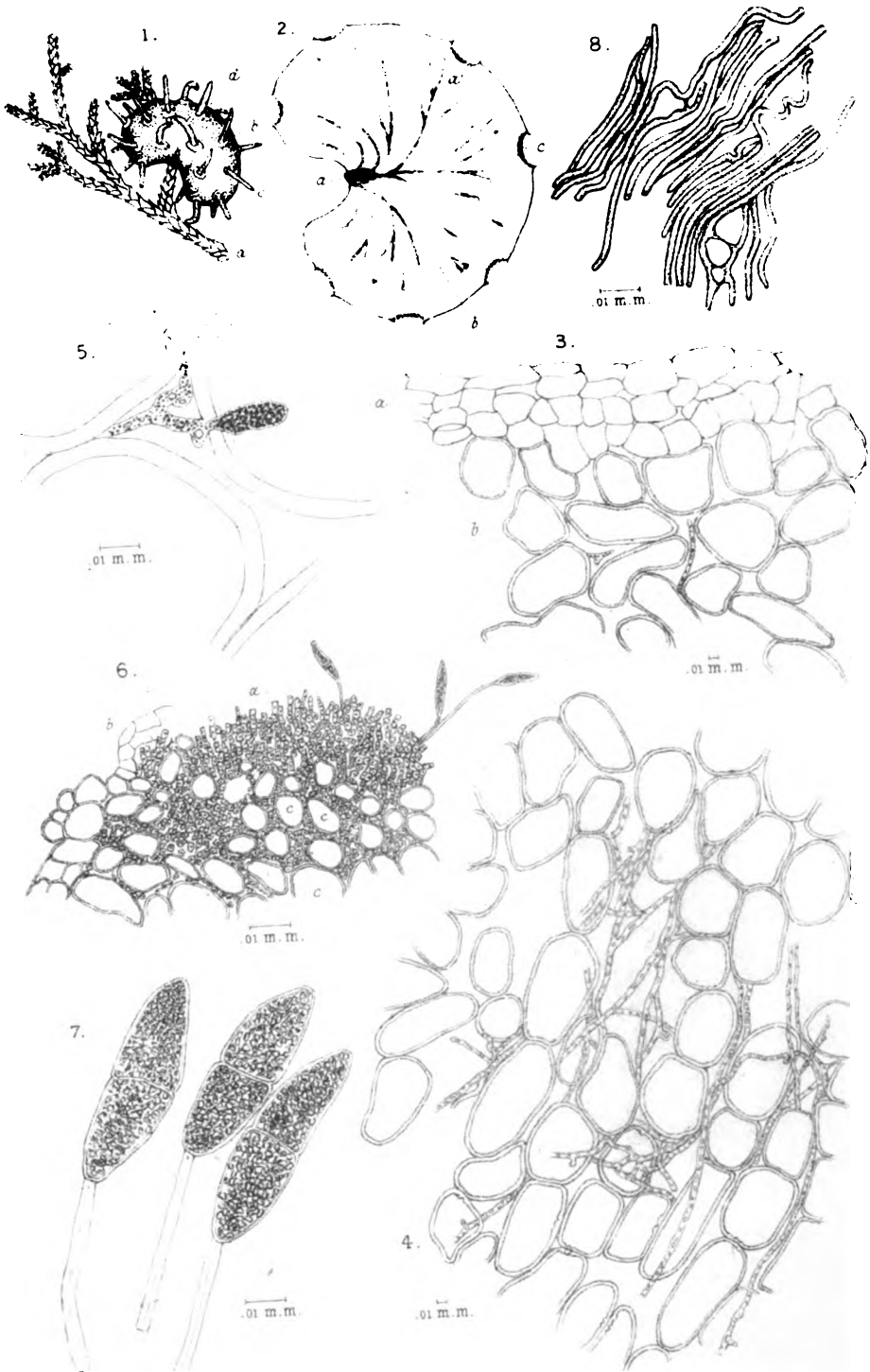
Fig. 4. Cross-section of parenchyma of the knot showing the fungus-mycelium.

Fig. 5. A haustorium.

Fig. 6. Section of the knot at the base of a spore-mass. *a*, Line of attachment of the spore-mass. *b*, Some epidermal cells of the knot. *c*, Parenchymatous cells of the knot.

Fig. 7. Spores of the fungus.

Fig. 8. Hyaline filaments of the spore-mass.



University Press, Oxford

On some Normal and Abnormal Developments of the Oophyte in Trichomanes.

BY

F. O. BOWER, D.Sc.,

Regius Professor of Botany in the University of Glasgow.

With Plates XIV, XV, and XVI.

INTRODUCTION.

THE relation of the Vascular Cryptogams to the Muscineae is a matter which is now more than ever before the minds of botanists; but the position of investigators is such that, while the grounds on which an opinion may be based are gradually becoming more consolidated, still new facts bearing on the point will be received with interest. The recent investigations of Treub and others on the oophyte of the Lycopods, and of Goebel on the prothalli of certain Hymenophyllaceae, serve to indicate that, though the characters of the spore-bearing generation (sporophyte) have hitherto formed the chief basis on which the affinities of the Vascular Cryptogams have been recognised, it is very essential to acquire a knowledge of and to compare the sexual generation (oophyte) of the various groups of plants in question, and to apply such knowledge as a check upon the results otherwise obtained. As we descend in the scale, and approach those forms in which the sporophyte is less conspicuous, while the oophyte is more prominent, it is natural to expect that the characters of the oophyte will be of relatively greater taxonomic importance, and this is in

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some measure the case in the Hymenophyllaceae, to which the observations now to be described relate.

The opinion has long been held that, regarding the series of Ferns alone, we find in the family of the Hymenophyllaceae the closest affinity to the Mosses: thus Presl, in 1843, expressed the view, previously indicated by Sprengel and others, that the Hymenophyllaceae constitute a link between these two groups; his opinion was, however, based exclusively upon the characters of the sporophyte, and it is only to be expected that prior to the discoveries of Hofmeister this should have been the case. It was Mettenius[1] who first supplied a connected account of the prothallus in these plants, and pointed out the similarity which exists between the prothallus of species of *Trichomanes* and the protonema of Mosses. Since 1864 little has been done; Janczewski and Rostafinski[2] wrote a description (without illustrative figures) of the prothalli of *Hymenophyllum Tunbridgense*; Cramer[3] described certain peculiar gemmae, borne together with sexual organs on filamentous prothalli, presumed to belong to *Trichomanes*; Prantl's work on the Hymenophyllaceae[4] is almost exclusively devoted to the sporophyte. It is, in fact, only quite recently that a substantial addition of well-founded facts has been made to the knowledge of the oophyte of the Hymenophyllaceae in a paper by Goebel[5]. Even there the prothallus of *Hymenophyllum* is much more fully described than that of *Trichomanes*, and in no single species can it be considered that we have knowledge even approaching to completeness.

Assuming that readers will have made themselves acquainted with the works above alluded to, I may proceed at once to the description of observations which I have recently made

[1] Ueber die Hymenophyllaceæ, 1864, p. 488.

[2] Sur le prothalle de l'*Hymenophyllum Tunbridgense*, in Mém. Soc. Cherbourg, 1875.

[3] Denksch. Schw. Nat. Ges. Vol. xxviii. (1880).

[4] Unters. z. Morph. d. Gefässkryptogamen, Heft i. 1875.

[5] Morphologische und Biologische Studien, in Ann. du Jard. Bot. de Buitenzorg, vol. vii. p. 74, etc.

on the prothalli of species of *Trichomanes*, merely remarking, by way of preface, that the characters to be described fall under two heads: *normal characters*, including the development of the prothallus, formation of sexual organs, &c.; and *abnormal characters*, including the phenomena of apospory and apogamy. Further, observations on sporophytic budding and oophytic budding by means of *gemmae* will be described.

I propose, first, to describe a species in which the course of development shows but slight deviations from that which is normal for Ferns generally, viz.

TRICHOMANES PYXIDIFERUM, LINN.

Description of Protonema[1].—This plant produces mature spores in the normal manner. They may germinate in the sporangium, or, having escaped from the sporangium, in the cup-shaped indusium, as has been described in other species[2]. On the mode of normal germination I have no details to add to those given by Mettenius, Goebel, and others. The result of germination is a much-branched, filamentous, protonema-like prothallus, coarser in texture than that of an average Moss, from which it can therefore be readily distinguished. The filaments are partitioned by septa, which are usually transverse, into cells, of which the length is not greatly in excess of the breadth, while a central swelling gives them a barrel-like form. Of the lateral branches (of which each cell may produce one, though it is by no means constantly developed), some retain and repeat the characters of the parent-filament,

[1] The material upon which these observations are based was derived from the collection in the Royal Gardens, Kew, where the method of cultivation of the Filmy Ferns in closed wall-cases and at a moderate temperature has attained signal success. It may be objected that it is impossible to be sure of the identity of species in cultures conducted in cases containing more than a single species; but I have made observations on the aposporous prothalli of the same species (which are described below); others on prothalli produced by germination from spores still in the sporangium or sorus; and these correspond so closely in character to the dense protonemal mat which was found overgrowing the stump, on which the specimen in question was cultivated, as to leave no doubt in my mind that the prothalli now described are actually those of *Trichomanes pyxidiferum*.

[2] Goebel, l. c. p. 92.

forming plentiful chlorophyll; others assume a brown colour, and, either with or without further branching, perform the function of rhizoids. The whole prothallus thus forms a much-branched matted growth, rising to a height of about a quarter of an inch. In its general aspect it appears to the naked eye not unlike a stiff-growing *Vaucheria*, and its filaments under a low power resemble a *Cladophora*. I have never seen the filaments of this species widen out into flattened expansions like those of *Trichomanes alatum*, to be described below, or of *Tr. sinuosum* and others described by Mettenius. In point of the filamentous form, the localisation of growth near the apex of the filament, the absence of intercalary growth, and in the branching not being restricted to one plane, as well as in the absence of flattened expansions, the protonema of *Tr. pyxidiferum* corresponds to the description given by Goebel for *Tr. diffusum*, Bl. and *Tr. maximum*. These species differ, however, from *Tr. sinuosum* as described by Mettenius[1] and *Tr. alatum*, as I shall show later, for in them flattened expansions of considerable size are commonly to be seen.

Special interest attaches to the position of the rhizoids relatively to the filaments which bear them. They are in most cases clearly lateral, and correspond in position to the other lateral branches of the protonema; finely-graduated intermediate steps, however, may be found from the lateral to the terminal position (Fig. 7, *a–d*), thus illustrating how members usually lateral may under circumstances undergo a gradual displacement so as to assume a position actually on the apex of the member which bears them. This observation has its bearing upon the question of the possible terminal leaf.

Apospory.—On old fronds a dense tuft of such protonemal prothalli as those above described may be seen projecting from the cup of the sorus; and as the germination of the spores is known to occur in the cup, or even in the sporangium itself, this might be considered a sufficient explanation. But if

[1] l.c. Taf. v.

longitudinal sections be cut traversing the placenta, it will be seen that towards the base of the sorus the sporangia are of smaller size, many of those lowest down showing various degrees of arrest, corresponding to their basipetal order of development. As the frond grows old, these may resume activity of growth, which, however, does not result in the formation of normal sporangia with spores, but of irregular masses of tissue, which differ widely in appearance from normal sporangia (Figs. 2, 3, 4). These irregular masses may then produce, by direct vegetative outgrowth, rhizoids, *r*, similar in appearance to those of the normal protonemal prothallus, and finally a filamentous protonema. Growths similar in nature, though often extremely irregular in form, may arise from the tissue of the placenta itself (Figs. 5, 6). In old fronds, where the general mass of the placenta has lost its activity, and turned brown, these growths are easily distinguished by their colour. It is thus seen that in *Tr. pyxidiferum* irregular initial growths, derived by direct vegetative outgrowth of the tissues of the sporophyte, may form the starting-point for the production of the protonemal oophyte; in fact, there may be traced a transition from the one generation to the other by a purely vegetative process, without the intervention of spores. This has elsewhere been termed the process of *apospory*, and it is here again, as in the examples previously described, associated with a *partial sporal arrest*[1]. It is to be regarded as a possibility that in other cases where a germination of the spores within the sporangium or sorus has been described, more careful investigation may disclose a similar aposporous development.

A Doubtful Vegetative Production.—In various other species of *Trichomanes* a vegetative multiplication of the oophyte by means of gemmae has been described[2]. Although I have examined a very large number of specimens of the protonema

[1] Compare Bower, on Apospory and Allied Phenomena, in Linn. Trans. Vol. iii. Part 14, p. 302, &c.

[2] Mettenius, l. c. Taf. v.; Cramer, l. c.; Goebel, l. c. p. 95; also a preliminary note by Bower on *Tr. alatum* in Annals of Botany, Vol. i. No. II (1887).

of *Tr. pyxidiferum*, I have found no trace of gemmae similar to those described for other species; but occasionally I have seen filaments assume a moniliform appearance, as shown in Fig. 8, and this is associated with a greater development than usual of those fungal hyphae, which are as constantly present in this plant as in other allied forms[1]. It is possible that the moniliform development is merely a pathological condition; its appearance, however, is suggestive of that segmentation of the protonema into spherical cells which is recorded as a mode of vegetative propagation for the protonema of *Funaria hygrometrica*. On this point, however, I am not in a position to give a decided opinion.

As to the nature of the fungus which infests the protonema in this species, it seems probable that it belongs to the series of the *Mucorini*. Its hyphae grow in close contact with the outer surface of the protonema, but haustoria projecting into the cells have not been observed.

Sexual Organs.—Our knowledge of the sexual organs in the genus *Trichomanes* is based on the observations of Mettenius, Cramer, and Goebel. Although the general form and position of the antheridia and archegonia have been described for several different species, the details of their structure and development are but insufficiently known. The description now to be given is far from being complete, still it will fill some gaps in our present knowledge, and also will have some value as relating to a species of this variable genus in which the sexual organs had not hitherto been observed.

The *antheridia* are produced laterally on the protonema, either singly or in pairs, as shortly stalked spherical bodies. They occupy a position corresponding to that of the lateral branches. I have never seen them associated with the archegonia, as described and figured by Mettenius for *Tr. sinuosum*[2], nor indeed have antheridia and archegonia been noted on the same branch-system; still, owing to the difficulty of tracing a complicated and interwoven protonema throughout its whole

[1] Goebel, l. c. p. 95.

[2] l. c. Taf. v.

length, it is impossible to speak definitely as to the distribution of the sexual organs, though my impression is that the species is dioecious.

The mature antheridium is a shortly-stalked body with a round head (Fig. 9, D); the stalk consists of a single cell, cut off by a septum from the cell of the filament which produced it, but the septum is often slightly above the actual point of insertion on the filament (Fig. 9, B, C, E) The head consists of a peripheral layer of tabular cells, which encloses a spherical mass of mother-cells of the spermatozoids (spermatocytes); these show characters similar to those of other Ferns, and have been seen to escape through a rupture near the apex of the antheridium. The spermatozoids have not been seen in motion. In point of development and succession of cell-divisions, the antheridium. as seen in optical section, shows some similarity to that of other Ferns; thus, after the spherical head is partitioned off from the stalk, a central cell is cut off from those which go to form the peripheral layer, by walls arranged as seen in optical section in Fig. 9, B, C. The actual position and succession of these walls is somewhat difficult to define. Observations of the young antheridium in the solid (i.e. from without, as in Fig. 9, E, F) point against the formation of a funnel-shaped wall, such as is described for the antheridia of most Ferns[1]; it would rather appear that segments, without any definite order of succession, are cut off by obliquely anticlinal and convex walls (Fig. 9, B); that these are succeeded by a dome-shaped periclinal wall (Fig. 9, C); the outer cell thus cut off may further divide by irregularly arranged walls (Fig. 9, E, F) into cells, which are indefinite in number and form. The appearance represented in Fig. 9, E, and to some extent also in F, would suggest at first sight a succession of segments cut off from a wedge-shaped apical cell; but young antheridia seen in optical section do not support this view (Fig. 9, B, C). Comparing these results with those obtained by Cramer[2] in his presumable *Trichomanes*, it will

[1] Kny, in Monatsbr. der Kongl. Akad. Wiss. Berlin, 1869. Id. Pringe. Jahrb. 1872; etc.

[2] l. c. Taf. i. Fig. 9 *an.*

be seen that the main features are the same in both species, especially with respect to the external appearance suggesting a number of segments cut off from an initial cell. Again, in the antheridia of *Hymenophyllum Smithii* described and figured by Goebel[1], an alternation of the basal walls is indicated, not unlike that which appears to obtain in *Tr. pyxidiferum*.

In the case of the antheridia above described, we should be justified in regarding the whole antheridium with its pedicel as replacing a lateral branch, the terminal cell of which is represented by the head of the antheridium.

The *archegonia*, on the other hand, are borne on massive growths (archegoniophores), which may be held in some cases to represent the apical cell of a lateral branch (Fig. 10). or the whole of a lateral branch (Figs. 11, 12). In one case, however, which has a special interest, the mass of tissue on which the archegonia are produced is obviously the result of partition of a single cell of a filament, without any marked increase of size having taken place (Fig. 13). This may be regarded as the simplest form of an archegoniophore hitherto described in any Fern, or even in any Bryophyte, and it approaches near to that suggested by Goebel[2] as the simplest possible, in which the sexual organs would be inserted directly on the protonemal threads. Thus, while there is an entire absence of flattened developments on which the archegonia might be borne, as described for some other allied forms[3], the actual position and origin of the archegoniophore is subject to some variation. Further, the cell-divisions (as far as I have been able to trace them) which give rise to these massive growths follow no definite order; this may be gathered from a comparison of the specimens represented in Figs. 11, 12, 13, 14. A wedge-shaped cell is sometimes to be seen at the apex of the growth, but, even if this be a true initial cell, its activity is not long continued, nor is it always to be found (Fig. 13).

[1] l. c. Taf. xiii. Fig. 89. Compare also diagram, Taf. xiii. Fig. 82.
[2] l. c. p. 94.
[3] Cf. Mettenius, l. c., *Tr. sinuosum*, etc.

The archegoniophore may bear numerous archegonia, and I have not been able to discover any definite succession in their appearance; thus, in Fig. 10, the archegonia (*a–e*) do not show any definite arrangement according to age. The first archegonium may make its appearance while the archegoniophore is still a small body consisting of but few cells (Fig. 11). In point of details of structure the archegonia correspond to the type usual for Ferns: the neck, which is straight, consists of four rows of cells (*a* Fig. 10, Fig. 15), the number of cells in each row being usually five (Figs. 10, 16), but the total may be six or seven (Fig. 11), and may vary in the different rows of the same archegonium (Fig. 17). The last divisions appear in the terminal cells of each row, and the walls are there somewhat irregularly disposed. The venter of the archegonium is embedded in the tissue of the archegoniophore. The central series of cells consists, at maturity, of a single canal-cell, a ventral canal-cell, and the ovum; there is nothing to be observed in these cells, or in the neck itself. which would lead to a closer comparison of these archegonia than those of any other Fern with the archegonia of the Bryophyta. The wall of the neck-cell undergoes the usual mucilaginous change, and finally the apex of the neck is ruptured in the usual way (Figs. 10, 15).

The actual process of fertilisation I have not been able to observe. The method of cultivation in uniformly damp air, and without watering from above (excepting very occasionally), will tend to prevent the sexual process in the Kew cultures; nevertheless a few young seedlings have been found connected with the archegoniophores, thus showing that the sexual act does take place; but the fragmentary observations which I have been able to make on the embryology are too incomplete to warrant their present description. A detailed account of the development of the embryo, especially in the rootless forms[1], is a desideratum which it is hoped that future observations may supply.

[1] A list of these is given by Mettenius, l. c. p. 409.

Sphorophytic Budding.—When the fronds grow old, there may be seen an additional mode of propagation, by direct budding from them, which results in the formation of new sporophytes. These growths appear on the lower surface of the frond, and are commonly associated with the ribs; or they may occasionally be found at any point on the thin lateral parts. To the naked eye they appear at first as brown velvet-like patches, consisting chiefly of dark-coloured rhizoids (Fig. 18). A section through such a frond, on which sori may be entirely absent (Fig. 19), shows that these growths begin by the extension and division of single cells. I have been unable to trace any regularity in the succession of divisions, or direction of growth, but the result is the formation of irregular filaments, bearing numerous brown rhizoids, and enlarging sooner or later into massive growths (Figs. 20, 21, 22, 23). These ultimately acquire the characters of a sporophytic axis, bearing leaves which are at first of simple form, as is the case with the first leaves of the sexually produced embryo in this and other species. Although their development corresponds in some points to that of the buds described in other Ferns by Heinricher[1], the initial filamentous stage makes a different interpretation of them possible, and this point will be further discussed at theconclusion of this paper. Meanwhile, however, it is to be noted that they originate at points quite apart from the sori, and they appear to have no connection with any sporal arrest.

Trichomanes alatum, Sw.

My attention was called some months ago by Prof. Dickson to a peculiar development on the tips of the older fronds of a specimen of *Trichomanes alatum*, which was growing in the Edinburgh Botanic Garden. This peculiarity had been noted by him some time before, and a drawing made from another specimen in the private collection of Mr. Neill Fraser showed that the development is not restricted to the single indi-

[1] Sitz. d. Akad. Nat. Wiss. zu Wien, July, 1878.

vidual alone. I take this opportunity of acknowledging my obligation to Prof. Dickson for handing over to me material for an investigation in which he had already interested himself. Work was begun on the Edinburgh plant, and the results acquired from it are briefly stated in the Annals of Botany, Vol. I. No. II. Since that note was written I have had the advantage of making comparison with the magnificent specimens growing in Kew, and it is found that not only do they show similar peculiarities to those of the Edinburgh plants, but even further abnormalities which will be described below. The conclusion to be drawn is, that, since in three different collections plants of this species show similar peculiarities, these are to be regarded as frequent, or even constant characters.

Aposporous Growths.—The sori of those specimens which I have examined frequently produce normal sporangia with mature spores; but the great majority of the prothalli which I have observed were produced, not by germination of spores, but by peculiar aposporous growths, which arise in remarkable profusion from such old fronds as have fallen to the ground, or even from the tips of pinnae of fronds, which still retain their normal position.

As to the mode of formation, point of origin, and structure of the prothalloid organs, which are produced by direct vegetative outgrowth from the frond, there is great irregularity. It may be stated at once that the resulting prothalli differ from those of *Tr. pyxidiferum* in the fact that, though they are often protonemal in form, yet flattened expansions, one layer of cells in thickness, are of common occurrence (Fig. 25), while a succession of these may be connected by protonemal filaments so as to form a very complicated and irregular whole (Fig. 24). This may be compared with the description and figures given by Mettenius for *Tr. incisum*[1].

These irregular prothalli may originate directly from the frond in various ways: thus, single cells of the apex of the pinna (Fig. 26), or of its margin (Fig. 27), may grow out into

[1] l. c. Taf. v. Fig. 1 and p. 492.

long filaments, undergo segmentation, and assume the characters of a branched protonema; or again, such growths may occasionally be produced from the surface of the frond, especially in connection with the nerves (Fig. 28), but this origin from the surface is less common. Occasionally filamentous growths arise from the sporangium, and it is difficult at times to distinguish between the intra-sporangial germination of spores and growths from the wall or annulus of the sporangium. In the case shown in Fig. 29, the latter origin seems to be the true one, since the central cavity is filled with an ill-defined brown mass, such as is seen in sporangia in which the development of spores is arrested; thus it is probably an example of aposporous development of protonema from cells of the annulus, following on sporal arrest. Sooner or later flattened expansions, one layer of cells in thickness, may be formed on these protonemal filaments.

Secondly, flattened outgrowths may originate directly from the frond of the sporophyte without the intervention of protonema. On old fronds it is not at all uncommon to find the tips of the pinnules produced into strap-shaped growths (Fig. 30), which assume an oblique or upright position, and are distinguished from the frond by the entire absence of the sharply-conical branched hairs, which are so characteristic of the sporophyte in this species, and by the want of any midrib with a vascular bundle[1]. At their upturned apices tufts of 'sterigmata'[2] may be seen, bearing gemmae. It will be shown

[1] In this plant it has at times been difficult to distinguish between the thin flattened prothalli and the thin lateral portions of the fronds which produce them, and resemble them closely in structure and arrangement of the cells. A constant character of the frond of the sporophyte in this species is the presence of branched hairs with sharp apices and thickened walls (Fig. 24); these differ essentially both in the mode of branching and in the sharpness of their apex from the protonemal filaments or rhizoids, which are formed on the prothalli; and the presence of these branched conical hairs may be taken as a diagnostic character of the sporophyte from the oophyte: without this mark the distinction of the two generations would often be difficult, and especially so in the specimens of apogamy to be described later.

[2] The term 'sterigma' has been adopted by Goebel (l. c. p. 82) for the pedicels which bear the gemmae.

later that these are characteristic reproductive organs of the oophyte, and their presence serves to strengthen the conclusion that in these strap-shaped growths from the margin or tip of the pinnule we have to deal with prothalloid developments produced in an *aposporous* manner.

But it is not only the marginal cells of the frond which may give rise to protonemal filaments; it appears also that any marginal cell of one of the ribbon-shaped prothalli may do the same: this is shown in Figs. 32, 33. Between the filamentous (protonemal) and flattened (prothalloid) forms intermediate steps may be found: thus, in Fig. 31 is shown a growth from a single marginal cell of the frond, which passes over almost at once into a narrow flattened ribbon; again, in Fig. 30, the right-hand branch consists of only two rows of cells, and this may be compared with Fig. 35, which is in part of its length a simple filament, but two of the cells have divided longitudinally, so as to show a transition to the flattened form. In face of these examples, which are only a few from the many observed, it is clear that there is little or no regularity of form or of place of origin in these prothalli, and that no sharp limit exists between the simple protonemal filament and the flattened expansion.

Passing on now to further details, the typical protonemal filament consists of a simple row of cells of variable length (Figs. 27, 34); the septa dividing them are transverse, or very slightly inclined, and show a striated appearance in optical section. In some filaments each cell may produce one lateral outgrowth with considerable regularity (Fig. 34); occasionally more than one may arise from each cell; or such appendages may be absent from a considerable proportion of the cells. These growths may develop in different ways: the large majority of them may remain of small size, and, turning brown, acquire the character of rhizoids (Figs. 33, 34); or they may repeat the characters of the parent filament as protonemal branches (Fig. 33 *p*); or again, they may develop at once as flattened expansions (Fig. 34 *x*). The cells of the protonema are crowded with chlorophyll-corpuscles, and each

contains a single nucleus. The transition from the simple filamentous protonema to the flattened expansion is sometimes gradual (Fig. 31); but in most cases it is sudden, and occurs at the apex of the filament (Figs. 28, 33, 35, 36). The succession of cell-divisions is more regular in the early stages of formation of the flattened ribbon than at any other time; thus, it will be seen how in Fig. 35 the filament has widened laterally, and two of its cells have divided longitudinally, while the terminal cell of the filament retains its position, the only modification being a slight curvature of its septum, which is a natural consequence of the lateral widening of the filament. The transition from this to the more advanced cases, shown in Figs. 28, 34, 36, is obvious enough, consisting chiefly in the farther lateral extension and segmentation of the cells already represented in Fig. 35. As the lateral distension proceeds, the curvature of the septum cutting off the apical cell may increase, and a change take place to growth with a two-sided wedge-shaped apical cell, as in the young prothallus of most Ferns; this is seen clearly indicated by the darker drawn anticlinal lines in Fig. 37; but this growth with an apical cell is of only short duration, and both the segments and the apical cell itself undergo partition by periclinal and anticlinal walls, and pass over to the condition of permanent tissue. The apex is not unfrequently elongated as an irregular terminal process, which may be regarded as a continuation of the original filament from which the expansion sprang (Fig. 39)[1]. These ribbon-like prothalli are never more than one layer of cells in thickness, and such appendages as rhizoids and protonemal branches are always produced from their margins, the surfaces remaining smooth. It may therefore be concluded from their form, distribution, and the arrangement of the cells composing them, that the development of the ribbon-like expansions is a simple variant on the filamentous protonema, and that its origin is based on a lateral dilatation of the simple filament.

Gemmae.—A marked phenomenon in connection with these

[1] Compare also Mettenius, l.c. Taf. v. Figs. 1 *a*, *g*.

most irregular prothalli is the formation of *gemmae*, or, as Cramer termed them, *conidia*. Such organs, borne on the oophyte in the Hymenophyllaceae on the tips of flask-shaped pedicels[1], were described by Mettenius[2] in *Trichomanes incisum* var. *Krausii*; but it does not appear that their germination was traced by him, or their true nature established; also, judging from our present knowledge of similar forms, it would seem probable that the gemmae observed by Mettenius were immature. Cramer, working with material of uncertain origin, but presumably belonging to some species of *Trichomanes*[3], described spindle-shaped gemmae, borne on flask-shaped stalks inserted on a filamentous, protonema-like growth; this protonema also produced antheridia, archegonia, and embryo plants, similar in their main characters to those described by Mettenius for species of *Trichomanes*. He further succeeded in tracing the germination of these gemmae, and thus established that they are vegetative organs of propagation of the oophyte. Quite recently Goebel[4] has described similar observations made on various Ferns, notably on *Vittaria parvula* and *Monogramme paradoxa*, in which the formation of spindle-shaped gemmae in large numbers on the margin of the thallus has been seen, and, in the former case at least, their germination noted. He has also described organs, probably 'sterigmata,' borne on the prothallus of an unrecognised species of *Trichomanes*, and in various species of *Hymenophyllum* the formation of adventitious buds, different it is true in their form, but subserving the function of vegetative propagation of the oophyte. As no one of these writers has given a record of the development of the gemmae, illustrated by figures, in any definite species of *Trichomanes*, it will not be superfluous to do so here.

[1] 'Sterigmata' of Goebel, l. c. p. 82.

[2] l. c., p. 493. Compare figures in Plate v.

[3] Denksch. Schw. Nat. Ges. 1880. This presumption is now strongly supported by the facts which have recently been published by Goebel, and by my own observations.

[4] Op. cit.

The gemmae of *Trichomanes alatum* are borne in the greatest profusion on the ends of the prothalloid growths. They may appear on those strap-shaped growths which are borne on the tips of the pinnae (Fig. 30), or at the ends of the secondary expansions (Fig. 25), or even in some cases they may be the product of simple filaments (Fig. 40), though this is less common. There is no reason to think that the gemmae borne in these different positions differ in the least in their real nature. Their development is in the following manner. Single cells of the prothallus assume first an elongated form (Fig. 41 [i]), becoming very soon enlarged at the apex into a spherical head (Figs. 41, 42 [ii]); this is subsequently cut off by a septum (Figs. 30, 41, 42 (iii]), the lower cell being the pedicel or sterigma, and the upper, or head, developing into the gemma; this now elongates transversely, or it may be in an oblique direction, and undergoes successive divisions by walls perpendicular to the axis of elongation (Figs. 30, 41, 42 [iv]), till the whole gemma is ultimately composed of five to seven cells; these become slightly barrel-shaped at the period of maturity, and are densely stored with reserve materials. Meanwhile a change takes place in the upper part of the sterigma; the cell-contents are for the most part transferred to the gemma, while a brown coloration of the wall appears near the apex. At this point the wall appears to be very brittle, and it is here that the gemma breaks away, often carrying with it a small portion of the sterigma (*x* Figs. 43, 44), which may still be recognised after germination has begun. When sown on damp soil, and kept at a moderate temperature, the germination of the gemmae is excessively slow; for instance, I have seen gemmae which have been cultivated on damp soil for six weeks remain quite unchanged, though still of healthy appearance. Owing to this very slow development I am not in a position to go further than to state that germination does take place (Fig. 44).

After a sterigma has produced a single gemma its function is over, and it does not develop further, but remains adherent to the prothallus, such old sterigmata being often seen in very

large numbers (Fig. 30). Even before the first gemma is mature, a fresh sterigma may begin to be formed at the foot of the first (Fig. 41) as a papillar outgrowth. The succession of sterigmata thus formed is not unlike that of the antheridial cells on the branched hairs of *Fucus*.

It will now be evident that in all essential points the formation of gemmae above described as occurring in the aposporous prothalli of *Trichomanes alatum* corresponds to that described for the prothalli of the presumable *Trichomanes* by Cramer; further that there is in it nothing at variance with the less complete accounts of similar formations given by Mettenius and by Goebel for other species. The conclusion to be drawn is, that the formation of gemmae is a wide-spread phenomenon in this genus.

Sexual Organs.—It may be objected, on the ground of the description above given, that it is mere assumption to say that the protonemal filaments and flattened outgrowths observed are really of an oophytic nature, and belong to the sexual generation; and it is true that no sexual organs have as yet been observed on the prothalloid growths derived from the Edinburgh plant; but the longer established plants at Kew provided numerous *antheridia*, which, though never observed in the perfectly mature state, are still very similar to those described for other species of *Trichomanes*. They are produced, with very few exceptions, on the protonemal filaments, occasionally also on the margins of the flattened expansions. *Archegonia have never been seen on any of the cultures of this species*, and the observations of apogamous budding, to be detailed below, lead me to regard it as possible that no archegonia are formed at all in this plant. However this may be, the general character of the protonemal and flattened outgrowths, the absence of vascular tissue and of the branched conical hairs so characteristic of the sporophyte, the presence of gemmae similar to those observed by others on the sexual thallus, and lastly the presence of antheridia, suffice to show, without any room for doubt, that the protonemal and flattened outgrowths truly represent the oophyte, even though they may be produced

from the sporophyte without the intervention of spores (apospory).

Passing to the description of the antheridia, these are produced for the most part on the protonema, either laterally (Fig. 45 B), or terminally (Fig. 45 A); usually they are lateral as in *Tr. pyxidiferum*, and are seated on a short pedicel. They have never been seen to produce mature spermatozoids in this species, and the central tissue appears in the large majority of cases to be atrophied; one or more of the cells at the apex of the antheridium is usually brown and apparently disorganised. These facts diminish in some measure the interest which would attach to the study of their structure, as these antheridia evidently do not attain a full normal development. Seen from the outside, the cells composing the wall of the antheridium are usually irregularly disposed, and form as elsewhere one layer surrounding the central mass; the cell-walls often run obliquely (Fig. 45 A, B, Fig. 46), while at or near to the apex is often to be seen a cell which appears like a biconvex apical cell (*x* Fig. 46)[1]. The idea that this actually does represent an apical cell from which successive segments have been cut off is supported by observations of antheridia in course of development (Figs. 47, 48, 49); but it is difficult to harmonise such arrangements as those here shown in the young state with the more mature structure sometimes seen in optical section in this plant (Fig. 50). It would be possible, combining these observations with Cramer's, to draw a comparison between these antheridia and those of the Mosses in respect of the arrangement of cells in the young antheridium; but, on the other hand, it must be remembered that the antheridia in this species do not come to normal maturity; that observations in *Tr. pyxidiferum*, in which the antheridia are normally matured, do not entirely accord with those on *Tr. alatum*; and that the order of the succession of septa does not appear to be constant in this species. On these grounds it cannot be held that these observations on the order of

[1] Compare Cramer, l. c. p. 8, Taf. i. Fig. 9 *an*.

segmentation of the antheridium will serve as perfectly trustworthy evidence of affinity to the Mosses; nevertheless the comparison is worthy of note.

Apogamy.—As above stated, no archegonia have been observed on cultures of *Tr. alatum*, nor have any archegoniophores, such as those of *Tr. pyxidiferum* and other species, been seen; nevertheless sporophytic buds are not of uncommon occurrence in connection with the flattened expansions (Fig. 51), and the question arose how these are formed. From the partial abortion of the antheridia, and entire absence of archegonia, a process of apogamous budding might be expected, and observation shows that this does take place, though with some variety in the details.

In some cases a filamentous pedicel projects from the margin of the flattened expansions (Figs. 52, 53); this bears a multicellular outgrowth upon which, as it enlarges, hairs are formed of the conical, thick-walled, sporophytic type above referred to (compare Fig. 24). The cellular mass, produced on such a pedicel, is at first of indefinite form, but becomes ultimately differentiated into parts which may be recognised as the first leaf, stem, and root of the young sporophytic plant. In other cases the sporophytic bud is not borne on a filamentous pedicel, but is inserted with a broad base upon the margin of the thallus (Fig. 54). Several of these specimens were carefully examined on both sides, and no archegonia were seen; when it is remembered that no archegonia in any stage of development have been noted in this species, and when this is associated with the hairy appearance of the buds from the very first (sexually-produced embryos being smooth), the above statement, together with the drawings, will, I think, suffice to establish the point that in the formation of these sporophytic buds archegonia do not take a part; in fact, that these buds are a direct vegetative development of the sporophyte from the oophyte in an apogamous manner. The minute details of development have not been followed out, partly owing to the want of sufficient material, partly for the reason that the growths are not uniform in their mode of

development, and because a knowledge of the details would not materially increase the interest in the process, at all events not until the normal development of the embryo is more perfectly known.

If further substantiation of the fact of apogamy in this species be required, it is to be found in the still more frequent cases represented in Figs. 55, 56. In these the exact converse is to be seen of those transitions from the sporophyte to the oophyte above described (Figs. 27, 30) in this plant. Here, without any distinct limit between them, the oophyte passes over into the characteristic sporophyte. This is particularly well shown in Fig. 55. At the base of the specimen branched protonemal filaments are seen attached, and the flattened thallus, with its marginal filaments, is quite a characteristic oophyte; passing upwards, however, a vascular bundle or rib is gradually formed at the centre, similar in position and nature to that of the normal sporophytic frond, while at the apex a number of the characteristic conical branched hairs are inserted. Fig. 56 demonstrates the transition even still more plainly, and shows the protonema, *pr*, at the base bearing an antheridium, *a*. The lower portion of the flattened thallus is characteristically oophytic, consisting of a single layer of cells with marginal protonema and rhizoids; passing upwards a transition is again seen to the flattened frond with midrib, marginal branched hairs, and characteristic apex, all of which characters stamp it as sporophytic. Further, a superficial bud, *b*, has been formed, having the characteristics of the sporophyte, and from it a vascular bundle, *v.b.*, extends downwards for a short distance into the prothallus, and finally ends blind. Sections were cut through this bud, and in Fig. 57, which is drawn from one of them, it is readily seen that the tissues of the sporophytic bud are continuous with those of the thallus, and especially that the tracheides of the vascular bundle, *tr*, pass down directly from the bud into the thallus. There can in these cases be no doubt as to the direct vegetative growth of the sporophyte from the oophyte. We may conclude with the utmost certainty that

these are examples of apogamy, the sexual process being entirely eliminated.

Conclusion.

Of the observations above detailed we shall do well to keep distinct from one another those which relate to normal processes, and those which may be regarded as abnormal; to the former category belong the observations on the conformation of the oophyte, on the antheridia and archegonia, and (perhaps) on the reproduction by gemmae and by sporophytic budding; these will have their comparative value; to the latter belong the observations on apospory and apogamy, which have rather a teratological, and generally physiological interest. The former will be first considered.

Goebel has recently given[1], in a tentative way it is true, a sketch of the possible phylogenetic development of the Hymenophyllaceae, based on the characters of the oophyte. He suggests that the phylogenetically oldest form of the oophyte was the branched cellular filament, on which the sexual organs were directly inserted, and notes that this form is still to be seen in many species of *Trichomanes* [e.g. our *Tr. pyxidiferum*], but with the archegonia inserted on a multicellular receptacle: this receptacle is in the present paper termed the archegoniophore. He regards as the next step the widening out of branches of the filamentous protonema into flattened expansions [as in *Tr. incisum* and *Tr. sinuosum*, described by Mettenius, and in our *Tr. alatum*]; on these flattened expansions the sexual organs are inserted in *Tr. incisum* and *Tr. sinuosum*. He suggests it as possible that these may have been first formed as expansions of the simpler archegoniophores, and that they ultimately became developed in point of time before the appearance of the archegonia, and he supports this view by comparison of other Vascular Cryptogams. He proceeds under his fifth head to state that 'the prothallus of *Hymenophyllum* arose from that of *Trichomanes*

[1] Morphologische und Biologische Studien, in Ann. Jard. Bot. Buitenzorg, 1887.

by the transfer of the formation of flattened growths from the lateral branches to the main axis of the prothallus, and accordingly the growth of the flattened surfaces has not remained so limited as is the case in the quoted species of *Trichomanes*.' This statement is supported by comparison of details in the two genera.

The question now is, how do the details of structure of the oophyte in the species above described fall in with this scheme, and how far are the characters, which Goebel makes use of, constant in the species? The latter question vitally affects their importance as evidence in tracing the phylogenetic connections of the family.

Apart from differences connected with abnormal development, the two species of *Trichomanes* above described differ from one another in details of conformation of the oophyte. In *Tr. pyxidiferum* flattened expansions have never been seen, the only departure from the simple filamentous (protonemal) form being in the case of the archegonium-bearing branches (archegoniophores). In the position of these latter there is some want of uniformity, the specimen in Fig. 13 showing the archegoniophore to be merely a modification of a cell (or possibly two cells) of the filament due to septation, while the archegoniophore is usually a lateral appendage in this species; this one specimen would therefore be a nearer approach than others figured by myself, or by other writers, to that possible type which Goebel has called 'die phylogenetisch älteste,' in which the sexual organs would be directly inserted on the branched filamentous oophyte, as in *Vaucheria* (l. c. p. 109). Thus, there is want of constancy in *Tr. pyxidiferum* in respect of one of those characters involved in Goebel's scheme.

In *Trichomanes alatum* [as also in *Tr. incisum* and *Tr. sinuosum* as described by Mettenius] great variety is to be found in the conformation of the prothallus. It is at times filamentous, and profusely branched; at other times, and without any apparent regularity, it widens out into flattened expansions, which, as above pointed out, are sometimes lateral in origin

(Fig. 34), but usually terminal (Figs. 35, 36). Thus, there is irregularity in this species with regard to the position of the flattened growths: this is again a character involved in Goebel's scheme.

Thus two of the characters cited in Goebel's phylogenetic sketch are variable, not only in the genus or species, but even on specimens derived respectively from the same individual parents. I apprehend that the value of characters for phylogenetic argument is in proportion to their constancy of occurrence; and accordingly these vegetative characters of the oophyte, which vary in different specimens derived from the same parent, or even in the individual specimen, cannot be considered as a sound basis for phylogenetic argument.

Now, it is impossible to deny that in our views of the relationships of the Vascular Cryptogams much greater importance has usually been attached to the characters of the sporophyte than to those of the oophyte, and botanists will welcome an attempt such as that of Goebel to place the comparison of the oophyte on a wider basis of detail. As a speculation on the course of evolution of the oophyte of the Ferns, Goebel's scheme may be accepted as, on the whole, a probable one; but the real question is whether any, and if so, which of the forms we now see living directly illustrate the original progression. Are they the result of degeneration, or may they not be immediately influenced in their development by present external conditions? I venture to think that in the comparative treatment of the oophyte of the Vascular Cryptogams even greater caution will be necessary than in that of the sporophyte, inasmuch as we have to deal here with a generation which we have every reason to believe is in its decadence, and is accordingly more subject to degradation and its consequent modifications, than the sporophyte, which is seen, so to speak, in the nascent condition in the Vascular Cryptogams. And, as in the Phanerogams we may, under peculiar circumstances, see the vegetative organs reduced both in internal and external complexity, so, though

in a less degree, it may be imagined that the oophytes of present Vascular Cryptogams may actually be a much more reduced type of sexual generation than some of their ancestors.

We know from direct observations that abnormal external conditions may largely control the vegetative development of the oophyte. Two pertinent examples of this may be cited in plants not far removed from those under discussion. The first is described by Dodel-Port [1], who found that when prothalli of *Aspidium violascens* are kept submerged, single cells at the margin or surface may grow out into confervoid filaments, some of which, as figured by him, show a marked similarity to the protonemal filaments of species of *Trichomanes*. The second case is one described by myself[2]. If the fresh gemmae of *Aulacomnion palustre* be grown in water, protonemal filaments are produced by outgrowth of single superficial cells, but no leafy buds are formed on the protonema; whereas, on damp soil, leafy buds are produced readily enough. Readers will doubtless be able to supply themselves with other parallel cases. In presence of such evidence, and in treating of organisms which are so insufficiently known as the oophytes of the Hymenophyllaceae [3], it appears to me that the greatest caution is to be maintained. We know that the Hymenophyllaceae are exceedingly susceptible to changes of dampness of the air, and may reasonably conclude that such changes may react upon their mode of growth. I therefore think that before we can with real security base phylogenetic conclusions upon details of external conformation of the oophyte in these plants, we require to know more of the characters of different species, and of the influence of

[1] Kosmos, 1880, p. 11.

[2] Journ. Linn. Soc. Vol. xx. p. 465.

[3] It is particularly to be noted that the conditions under which those specimens were grown, which have been used for the study of the oophytes of the Hymenophyllaceae, are insufficiently known. Mettenius worked from herbarium material; Rostafinsky worked on material collected in the open; Goebel's material was partly collected in the open, while the earlier stages were supplied by cultures. My own material has been chiefly grown at Kew in an almost uniformly damp atmosphere, low temperature, and in shade.

varied external conditions upon their growth. I would not be understood to question the main points of Goebel's theoretical sketch of the descent of the oophyte in the Hymenophyllaceae and other Ferns, and their relations to the Mosses, as given in the concluding paragraphs of his 'Studien'; but the detailed application to present forms is to be conducted with the greatest reserve. At present, as the result of my own observations, it appears to me to be probable that such features as the transition from the filamentous to the flattened form are due rather to the impress of external conditions under which the prothalli are grown than to inherited or ancestral characters.

Thus, while admitting the value of Goebel's comparative study of the conformation of the oophyte as a whole, I cannot think that comparison can be safely followed into details of the vegetative growth. Before we are in a position to do this, and draw phylogenetic conclusions from details of conformation of the vegetative oophyte of the Hymenophyllaceae or other Ferns, we require to be better acquainted with the prothalli of a larger number of species, to know more of the influence which external conditions may exercise upon them, and to make very liberal allowance for probable retrogression of development [1].

Because we may be doubtful as to the use of details of vegetative conformation in our comparison, there need be no objection to a comparison of a more general nature, based upon those characters which are more constant throughout the series of observed forms. Thus, the species of *Trichomanes* above described illustrate once more the general filamentous tendency of the oophyte in the genus, the resemblance of which to the protonema of the Mosses is too striking to be overlooked, and it is clear that, as regards the main points, the above observations fall in with the outlines of comparison of the oophyte as sketched out by Goebel. We may regard these filamentous prothalli as illustrating the affinity of the Hymenophyllaceae, and especially of the genus *Trichomanes*, to

[1] This Goebel admits (l. c. p. 116).

the Bryophyta. I should, however, be disposed to leave open, for the present, the question, whether or not the flattened expansions of species of *Trichomanes* and *Hymenophyllum* correspond to the flattened growths on the protonema of *Tetraphis* and other Mosses, as well as the still larger question of the relation of the Moss-plant to the archegoniophore of *Trichomanes*. There is, however, a strong presumption in favour of these comparisons. The main conclusion may be accepted, viz. that the protonema of the Moss corresponds with the protonema of *Trichomanes*; and this leads towards the conclusion given by Goebel in the following words, 'We may accordingly regard as the starting-point for the Bryophyta and Pteridophyta, Alga-like forms, consisting of branched filaments,' while it is also probable that in these ancestral forms the sexual organs were directly inserted on the filaments.

It is a well-known fact, illustrated now in more than one of the great series of Vascular Cryptogams, that the conformation of the oophyte may vary considerably in forms in which the sporophyte shows greater constancy. This has been pointed out by Treub in his studies on the Lycopodiaceae[1], in which he states his belief that the differences of conformation of the prothallus in various species of *Lycopodium* are not merely recently acquired. As reasons for this view he states that the differences are too great for that explanation, and that the young asexual generations are also dissimilar; he concludes that the different characters of the prothallus may in that genus serve as genealogical data. It must be admitted that the want of parallelism between asexual and sexual generations in the species of *Trichomanes* hitherto described is less marked than that in species of *Lycopodium*; but there is some similarity between the two cases, which is the more worthy of remark since the genera occupy somewhat similar positions with regard to the great series of the Bryophyta. Each is a near approach to the starting-point of a great series: in the one case the Lycopodinae, in the other the Filicineae. It is a

[1] Ann. Jard. Bot. de Buitenzorg, vols. iv–v.

striking fact that in both, though they differ so materially in details, there is great plasticity of conformation of the prothallus in the single species, as well as in different species of the genus; in both there is a filamentous tendency, and in both special organs of vegetative development of the oophyte are found. Since the question whether the differences of the oophyte, when the sporophyte shows greater constancy, be truly ancestral characters, or merely the result of comparatively recent special adaptation, affects both families, it deserves the greater attention. In view of the variability even in the single individual, and the want of constancy of succession of the various phases of development, I am inclined, at least in the case of *Trichomanes*, to the opinion above expressed, that the details of conformation of the vegetative thallus in this genus are not to be regarded as trustworthy genealogical data.

Passing on to the details of the oophyte in the species above described, the protonemal filaments are coarser than those of the Mosses, the septa transverse and the branching not perfectly regular, though in the majority of cases each cell produces a lateral outgrowth, which may develop as a new protonemal branch, a flattened expansion, or a rhizoid. When in *T. alatum* the protonemal filament widens out into a flattened expansion, the septa correspond at first in position to those of the original filament, though curved in accordance with the law of rectangular intersection; in some cases, however (Fig. 37), there are indications of the presence of a wedge-shaped apical cell, as in the Polypodiaceae, and this is worthy of note, since the figures of Mettenius, Cramer, and Goebel do not indicate such a structure in this genus; traces of it are to be found in the prothalli of *Hymenophyllum* described by Goebel.

Vegetative propagation of the oophyte, though apparently uncommon or even absent in *Tr. pyxidiferum*, is profusely present in *Tr. alatum*. The results obtained on the latter species place it beyond reasonable doubt that the observations of Cramer on spindle-shaped gemmae related actually to a species of *Trichomanes*. Not only do his figures and

description of the mature gemmae correspond very closely to my own, but also those showing the development; but whereas in Cramer's specimens the gemmae appear to have been formed on mere filaments, in *Tr. alatum* they are rarely formed on filaments, and more commonly on the apex of flattened expansions; this is, however, an unimportant difference. It cannot be doubted that Mettenius's figures[1] and those of Goebel[2] show early stages of development of similar gemmae. It may then be concluded that, though the formation of gemmae is not universally found in species of *Trichomanes*, it is at least a very general phenomenon. Referring to the process of oophytic budding generally, discoveries of recent years have shown that this mode of propagation is very widely spread among Ferns—a fact which tends further to establish the conclusion that the oophyte in Ferns is not merely a basis for insertion of the sexual organs, but is a generation leading an independent vegetative existence.

Though the external form of the oophyte may be liable to considerable variation in different species of *Trichomanes*, the form of the sexual organs shows more decided uniformity, and on this account may be considered to supply more trustworthy ancestral characters. As figured by Mettenius, Cramer, and Goebel, the antheridia are stalked spherical bodies, which in the mature state consist of a peripheral layer of cells surrounding a mass of mother-cells of the spermatozoids (spermatocytes). In point of their mature structure a comparison may be drawn between these antheridia and those of some Liverworts, e.g. *Radula* or *Trichocolea*; but the development of these, as described by Leitgeb, is dissimilar; there is also some similarity to the antheridium of *Sphagnum*. The study of the succession of the cell-divisions which lead to the mature condition presents some difficulties, owing partly to the density of the cell-contents in the young antheridium, partly to the fact that the antheridia of *Tr. alatum* are not fully developed in the normal manner. As above described, there are indications of an apical cell

[1] Taf. v. Figs. 8, 9.

[2] Taf. xii. Figs. 60, 61.

having the shape of half of a biconvex lens, from which segments are successively cut off; but I am not in a position to state that this is constantly the case, and it must be remembered that, even if it were, the development in this apogamous species is not normal.

In *Tr. pyxidiferum*, in which the antheridia develop normally, a similar appearance is seen on external observation of the antheridium (Fig. 9, *E*, *F*), but optical sections point to a succession of cell-divisions (Fig. 9, *A*, *B*, *C*), which does not support the idea of a wedge-shaped apical cell. It may further be noted that at least one of Cramer's drawings of antheridia[1] indicates the possible presence of an apical cell, while an alternation of segments cut off at the base of the antheridium has also been observed by Goebel[2] in *Hymenophyllum*. Thus, though the development of the antheridium does not appear to be perfectly constant in these plants, there are peculiar cell-divisions in it which do not coincide with those customary for Ferns. If an apical cell were actually present (and it must remain for further observations to decide this) it might be recognised as a character approaching that of the true Mosses; but at present this point cannot be closely pressed. Among the Ferns the succession of segments in the antheridium of *Osmunda* as described by Kny[3] approaches more nearly to that above described than is the case with those forms in which the funnel-shaped wall exists.

The description above given shows that the massive growths (archegoniophores) on which the archegonia are inserted do not conform to any strict type of origin, structure, or arrangement of cells in *Tr. pyxidiferum*. The view that the leafy 'Moss plant' may have arisen from an outgrowth of the protonema, such as the archegoniophore of *Trichomanes*, has been suggested by Goebel[4], and in the above observations I see nothing to cast doubt upon this; it is to be remarked, however, that, if we accept Goebel's proposed scheme, the specimen shown in Fig. 13 is a nearer approach than any hitherto described to

[1] l. c. Taf. i. Fig. 9 *an*.
[2] l. c. Taf. viii. Fig. 82.
[3] Prings. Jahrb. 1872.
[4] l. c. pp. 111, 112.

Goebel's ideal 'oldest type,' in which the sexual organs are inserted directly on the filament.

As regards the archegonia themselves, they correspond so closely to those of other Ferns as to supply no special evidence of a relation to other groups; thus (discounting the difficulty as to details of development of the antheridium) the sexual organs are more constant in their characters, and especially in their mature structure, than is the general conformation of the thallus, and accordingly greater weight should be attached to them than to the vegetative thallus in drawing phylogenetic conclusions. A comparison of these, on the one hand, with those of the other Ferns, and, on the other, with those of the Bryophyta, shows that, in respect of the sexual organs, the Hymenophyllaceae hardly approach nearer to the Bryophyta in any appreciable degree than do other Ferns.

Abnormal Characters.

Passing now to the abnormal characters, we see in *Tr. alatum* and *Tr. pyxidiferum* two fresh examples of *apospory*, accompanied by partial, though not complete sporal arrest. There are many points of similarity between these new cases and those of the Ferns described in my former paper on Apospory[1]; thus, the direct vegetative outgrowth of prothalloid expansions from the tips of the pinnae in *Tr. alatum* (Fig. 30), without there being any clear limit between the sporophyte and the oophyte, is closely comparable with the case of *Polystichum angulare*, var. *pulcherrimum* there described and figured[2]; again, the outgrowths from the surface of the frond (Fig. 28), and perhaps also from the sporangium itself (Fig. 29) in *Tr. alatum* find their parallel in the *Polystichum*. Even in the filamentous nature of some of the outgrowths of the *Trichomanes* (Fig. 27) a certain analogy may be traced to such growths as those shown in *Polystichum*[3]. It will be further noted that the outgrowth in *Tr. alatum*

[1] Linn. Trans. Vol. ii (1887), Part 14. [2] l. c. p. 308, Plate lviii.
[3] l. c. Fig. 36.

may arise apart from, or in connection with, the sorus, and in the former case either from the margin or the surface of the frond, and the same is the case in the specimens of *Polystichum*. The examples of apospory in *Tr. pyxidiferum* are much less profuse than in *Tr. alatum*, and are confined, so far as my observations go, to the sorus; but though the growth is here less frequent than in the other species, it is clear that the phenomenon of apospory does actually occur, for by direct vegetative outgrowth filaments are formed, which have been observed to bear antheridia.

That the discovery of new examples of apospory among the Ferns was to be anticipated has already been suggested[1], and if one family of Ferns might be thought more likely than another to supply such, it would be *Hymenophyllaceae*. In it the characters of the sporophyte and of the oophyte are more like one another, as regards structure and the circumstances under which they grow, than is the case in other families. The frond, like the flattened prothalloid growth, is only a single layer of cells in thickness, while both are extremely susceptible to changes of dampness of the air, and thus it might be reasonably expected that the sporophyte might run on directly by vegetative growth into the oophyte: more especially is this probable in specimens grown like those at Kew, in an atmosphere which is more carefully protected from changes of temperature and dampness than can possibly be the case in nature.

We have every reason to regard the oophyte of the Filicineae as the more ancient generation of the two: in the lowest forms of the series it was probably of littoral habit, growing where moisture was easily and constantly accessible, while without the presence of fluid water the sexual act in these forms could not be performed. Subsequently, by the more full development of the sporophyte, which is as a rule so constituted as to withstand greater changes of dampness and dryness, these lower forms spread to higher and dryer

[1] l.c. p. 322.

positions. It is further to be remembered that dryness is in most cases essential to the successful dissemination of the spores which it is the end and object of the sporophyte to produce, in order to multiply the species. Supposing now that the sporophyte and oophyte be continuously subjected to uniform conditions of moisture (and it is to be remembered that this is the habit of Hymenophyllaceae, and especially so for our Filmy Ferns under cultivation), there will be every reason to expect that the dissemination of spores will be in abeyance; the germination of the spores in the sporangium itself is a first step towards apospory, and this might very well lead to the direct vegetative outgrowth of the oophyte from the tissues of the sporophyte. More especially is this likely to occur where, as in Filmy Ferns, the structure of the two is more nearly similar than in other Ferns. The opinion may here be again expressed, and it is in no way shaken by the discovery of these new cases, that apospory is to be regarded as a sport induced by special circumstances, rather than as a reversion to an old type of development.

In the presence of apogamous budding in the same species (*Tr. alatum*) and even in the same individual which shows the phenomenon of apospory, we see a still further simplification of the life-cycle, which has, I believe, never been recorded in any other species. There is, I apprehend, no antecedent improbability that the two phenomena should occur in one and the same plant, and the fact that they do may be regarded as a coincidence rather than a point of further importance. A special interest attaching to this observation is connected with the light, which its record in a well-established case like the present will throw upon the case of *Isoëtes* described by Goebel[1]. In plants, which he found growing deeply submerged, the place of the sporangium was habitually occupied by a sporophytic bud, and Goebel offered the explanation that 'here there is obviously a case which belongs to the series of phenomena recently styled by

[1] Bot. Zeit. 1879, p. 1.

De Bary as apogamy, or loss of sexual function; only in the case above described the sexual organs are not arrested or lost, but the whole sexual generation.' In view of the fact that till the present time no example of coincidence of apospory and apogamy in the same species and individual has been described, this conclusion above quoted was a bold one; and even now in *Tr. alatum* the case is not exactly parallel. Here the sexual generation is not arrested; it is present and of considerable size, even the sexual organs are not entirely aborted, for, though no archegonia have been found, antheridia are far from rare. But notwithstanding that *Tr. alatum* is a much clearer case of the coincidence of apogamy and apospory in the same individual than the case of *Isoëtes*, its discovery will lend justification to the view expressed by Goebel,—a view which was previously based on less substantial grounds.

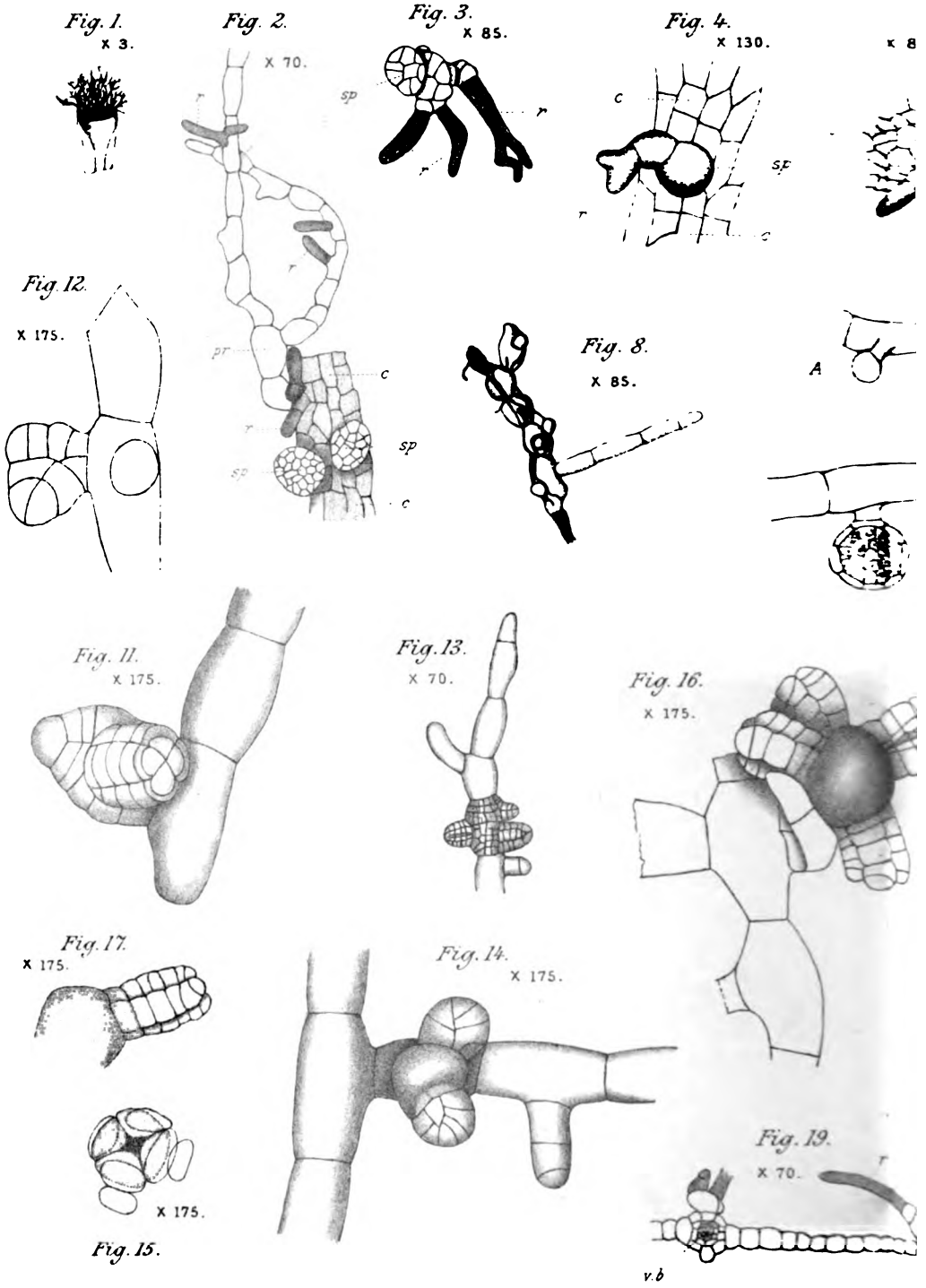
Apogamy is known to occur in the following Ferns:—*Pteris cretica*, in which it was first described by Farlow[1], and again by De Bary[2] in *Aspidium Filix-mas*, var. *cristatum*, *Aspidium falcatum*, and *Todea africana*[3]. These Ferns present the phenomenon in different degrees of completeness; though all bear more or less numerous antheridia (which at least in some cases produce mature spermatozoids[4]), archegonia are apparently altogether absent in *Aspidium Filix-mas*, var. *cristatum*, in *Pteris cretica* they are never fully developed, but in *Aspidium falcatum* and *Todea africana* they apparently attain maturity. Thus, of the Ferns above-named, the most complete type of apogamy is that shown in *Aspidium Filix-mas*, var. *cristatum*, in which archegonia are entirely absent, and the antheridia few; as to the actual formation of mature spermatozoids in this species I find no definite statement[5]. In the case of *Tr. alatum* the apogamy is quite as complete as, and apparently

[1] Q. J. M. S. Vol. xiv. p. 267. [2] Bot. Zeit. 1878.
[3] Sadebeck, in Schenk's Handbuch, Vol. i. p. 233, &c.
[4] De Bary, l. c. p. 459. [5] De Bary, l. c. p. 470.

even more complete than that of any of the cases cited above; the archegonia are absent altogether, while the antheridia, which have only been found in the Kew specimen, have never been seen to attain maturity, but show, over and above the absence of spermatozoids, a degeneration of certain cells of the wall of the antheridium.

It remains to notice the sporophytic budding produced on the old fronds of *Tr. pyxidiferum*. They originate from single cells apart from the sorus, and are at first filamentous, ultimately enlarging into the more massive tissues of the typical sporophyte. If the filament were of a protonemal character this might also be regarded as a case of simultaneous apospory and apogamy, the cycle being of a still more condensed or 'telescoped' type than in *Tr. alatum*; the characters of the filament will hardly bear this interpretation, and the examination of them has led me to the conclusion that in them we see nothing more than a peculiar form of sporophytic budding.

Finally, I regret to be unable to offer extensive evidence as to the permanency of these several phenomena, in the species named, or in the individual plant. The observation of the aposporous growths in three different collections may point to either of two conclusions: either it is a frequently recurring natural phenomenon in the species, or it is to be regarded as pathological; the latter is quite possibly the true explanation, and, as above suggested, the peculiarity may result from keeping the sporophyte constantly in an atmosphere saturated with moisture. A comparison of cultivated plants in many different collections with specimens taken from the natural habitats would be o value in the decision of this point.



F O.Bower del. TRICHOMANES PYx;

BOWER.—ON DEVELOPMENTS OF THE OOPHYTE IN TRICHOMANES.

Fig. 5.

x 85

Fig. 6.

x 85.

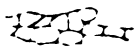
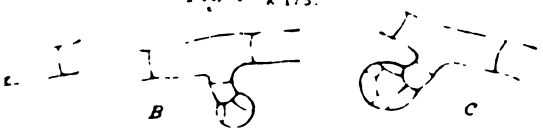


Fig. 7

x 85.

Fig. 9 x 175.



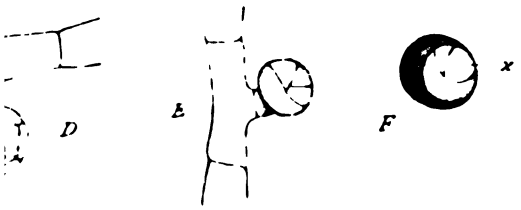


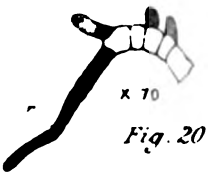
Fig. 10. x 175.

Fig. 23.

x 5.

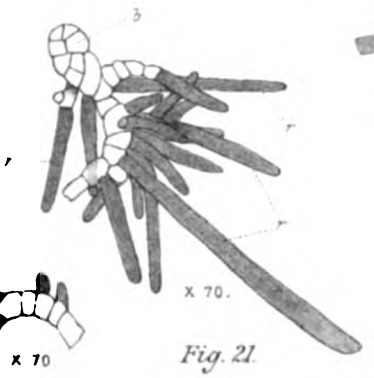
Fig. 18.

x 3



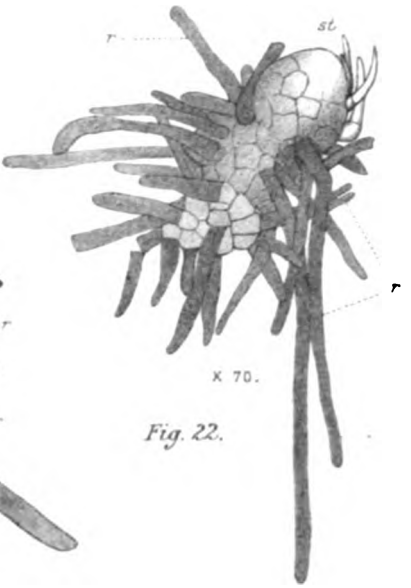
x 70

Fig. 20



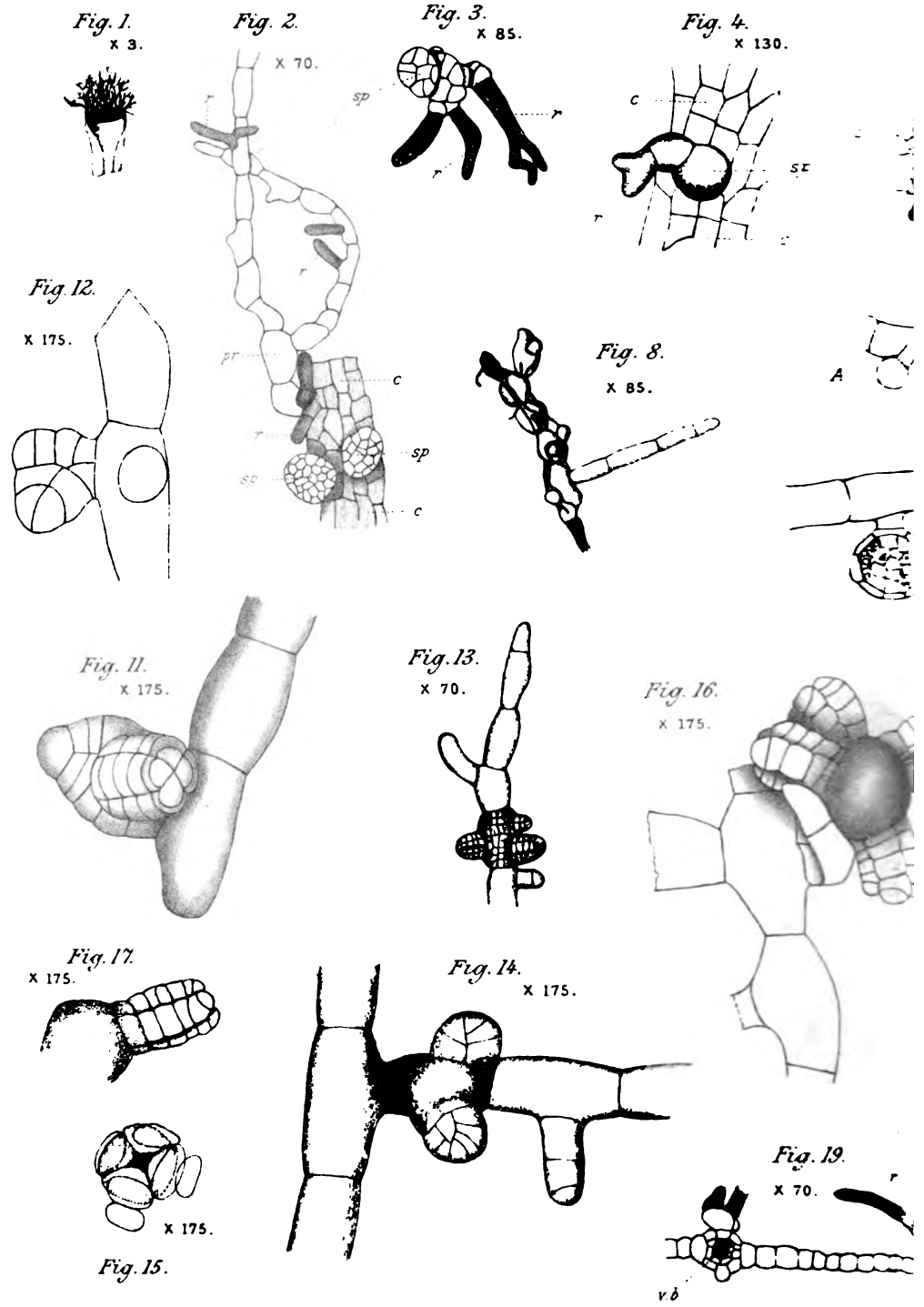
x 70.

Fig. 21.



x 70.

Fig. 22.



F O.Bower del.

TRICHOMANES PYx

BOWER.—ON DEVELOPMENTS OF THE OOPHYTE IN TRICHOMANES.

Fig. 5.

Fig. 6.
x 85.

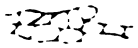


Fig 7
x 85

Fig 9 x 175

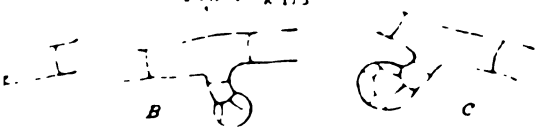
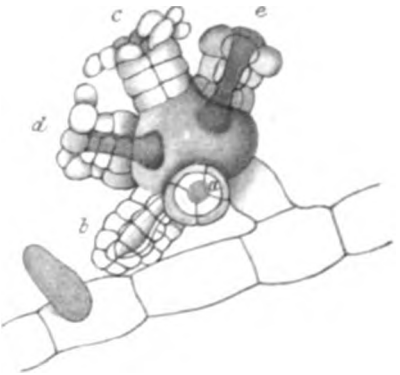


Fig 10 x 175



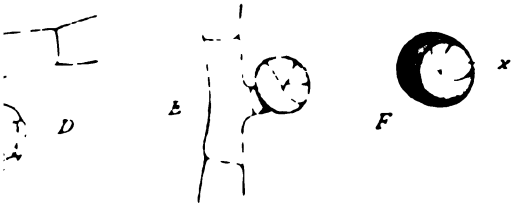


Fig. 23.
x 5.

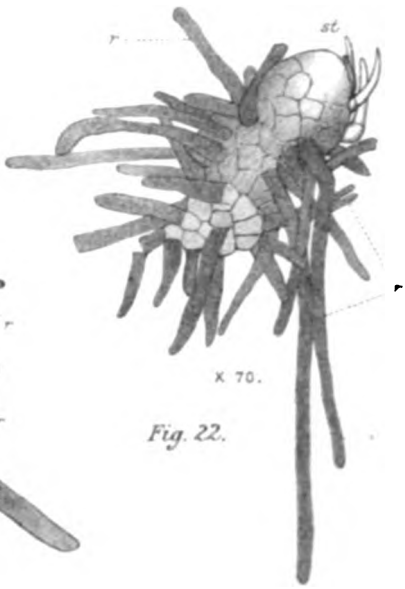


Fig. 22.

Fig 18.

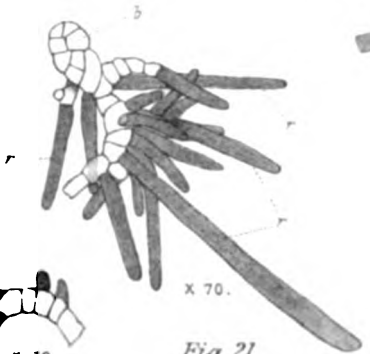


Fig. 21.

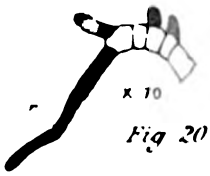


Fig 20

Fig. 24.
x 70.

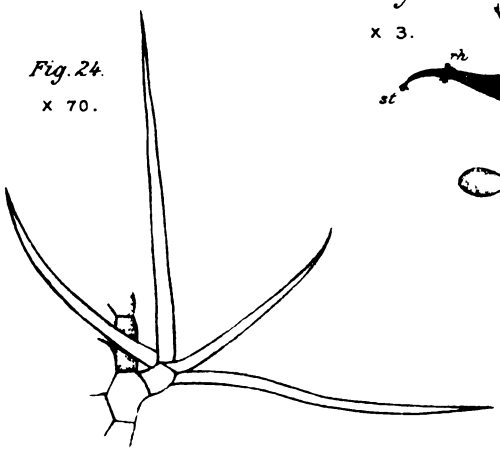


Fig. 25.
x 3.

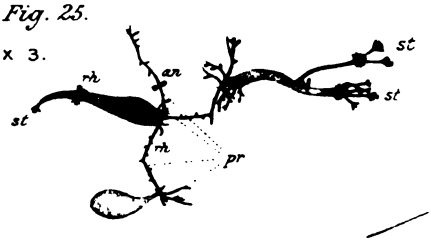


Fig. 28.

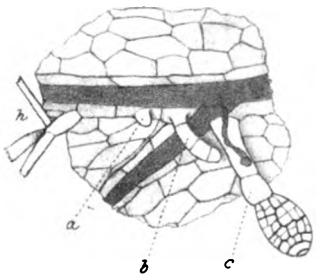


Fig. 30.
x 35.

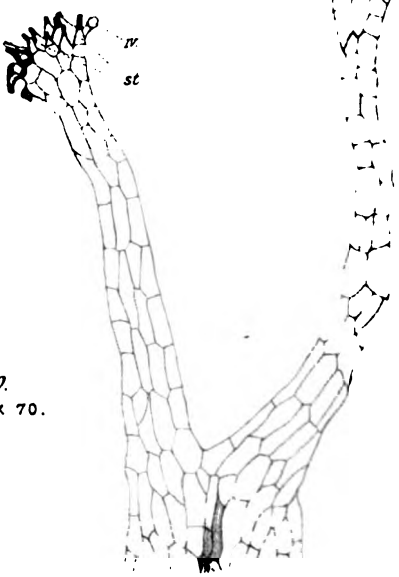


Fig. 37. x 85.

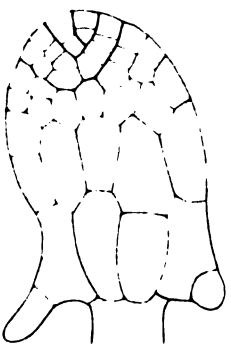


Fig. 40.
x 70.

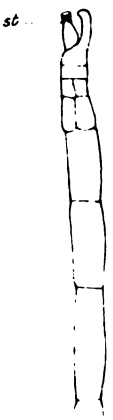
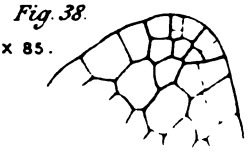


Fig. 38.
x 85.



F. O. Bower del. TRICHOM.

BOWER.—ON DEVELOPMENTS OF THE OOPHYTE IN TRICHOMANES.

Fig 27.
x 35.
Fig 29.
x 70
Fig. 35. x 35.
Fig. 31.
x 35.
Fig. 33.
x 35.
Fig. 36
x 70
Fig 32
x 3.
Fig. 41.
x 85.
Fig 34
x 35.

ES ALATUM, Sw

DESCRIPTION OF FIGURES IN PLATES XIV, XV, AND XVI.

Illustrating Professor Bower's Paper on some Normal and Abnormal Developments of the Oophyte in *Trichomanes*.

Figs. 1-22. Trichomanes pyxidiferum.

Fig. 1. Sorus from an old frond bearing filamentous protonema. × 3.

Fig. 2. Portion of the columella, *c*, bearing arrested sporangia, *sp*, which have undergone a further irregular growth. Protonema, *pr*, and rhizoids, *r*, have arisen by outgrowth of superficial cells of the columella. × 70.

Fig. 3. A sporangium, *sp*, which has been arrested in its normal growth and developed from it is an irregular growth with rhizoids, *r*. × 85.

Fig. 4. Columella, *c*, with arrested sporangium, *sp*, from which a rhizoid has been formed, *r*: the sporangium is multicellular, but the cell-divisions are not drawn in. × 130.

Fig 5. Irregular growth with rhizoids, *r*, from the columella, *c*. × 85.

Fig. 6. Part of a section through the columella, s owing outgrowth from a single cell. × 85.

Fig. 7. *a–d*. Series illustrating intermediate steps from lateral to terminal position of rhizoids. × 85.

Fig. 8. Old moniliform protonemal filaments, with fungal hyphae. × 85.

Fig. 9. A–F, Antheridia in various stages of development. B, C, D seen in optical section. E seen laterally from outside. F seen obliquely from above. *x*, centre of the apex. × 175.

Fig. 10. Branch of protonema (archegoniophore) bearing five archegonia of successive ages, *a–e*. × 175.

Fig. 11. Ditto, with one archegonium. × 175.

Fig. 12. Ditto, very young before formation of archegonia. × 175.

Fig. 13. A protonemal filament in which apparently one cell has become partitioned into a multicellular mass, on which are borne three archegonia. × 70.

Fig. 14. Young archegoniophore showing relation to the protonema which bears it. × 175.

Fig. 15. Neck of archegonium, as seen from above after it has opened. × 175.

Fig. 16 and 17. Archegonia showing variable number of cells composing the neck. × 175.

Fig. 18. Part of old frond bearing on its under surface numerous sporophytic buds. × 3.

Fig. 19. Part of transverse section of a frond showing outgrowths from single cells. × 70.

Figs. 20 and 21. Such outgrowths in later stages of development. × 70.

Fig. 22. A similar outgrowth from frond of more advanced development. × 70.

Figs. 23–57. Trichomanes alatum.

Fig. 23. A still more advanced sporophytic bud still attached to the frond which produced it; *l*, leaf; *st*, stem. × 5.

Fig. 24. Characteristic branched conical hair from frond of sporophyte. × 70.

Fig. 25. Oophyte of *Tr. alatum*, showing the relations of protonema, *pr*, to the flattened expansions, the antheridia, *an*, and rhizoids, *rh*, also old sterigmata, *st*. × 3.

Fig. 26. Tip of frond showing incipient outgrowth of single cells. × 70.

Fig. 27. Similar outgrowth more advanced, so as to result in protonema-filaments. × 35.

Fig. 28. Portion of a frond with branched rib, from the surface of which protonemal filaments, *a*, *b*, *c*, have been formed. *h*, one of the branched conical hairs of the sporophyte. × 35.

Fig. 29 Sporangium: a rhizoid, *rh*, and a protonemal filament, *pr*, have been formed, apparently from cells of the annulus. × 70.

Fig. 30. Aposporous development from the apex of a pinna. *v.b.* ending of a vascular bundle of the sporophyte. Both limbs of the oophytic growth have produced numerous sterigmata, *st*, and gemmae. × 35.

Fig. 31. Irregular oophytic outgrowth from margin of a frond. × 35.

Fig. 32. Flattened prothallus, one layer of cells in thickness, with numerous marginal protonemal filaments. × 3.

Fig. 33. Marginal protonemal filament, *p*, produced from a flattened prothallus, *prth*, and widening out at its apex into a second flattened growth, *prth II*. × 35.

Fig. 34. A characteristic piece of protonema of *Tr. alatum*: each cell forms a lateral appendage, which usually develops as a rhizoid, *r*. At *x* is a young flattened expansion placed laterally. × 35.

Fig. 35. A protonemal filament showing lateral extension, and division of cells by longitudinal walls: this is an early stage in the development of a flattened expansion. × 35.

Fig. 36. A further stage of a development of a protonemal filament into a flattened expansion: note that in both of these cases, as also in Fig. 28, the expansion is terminal in position. × 70.

Figs. 37–39. Apices of flattened expansions while young, showing arrangement of apical meristem. × 85.

Fig. 40. A protonemal filament which has borne a terminal sterigma, *st*: a second is being formed laterally below it. × 70.

Fig. 41. Sterigmata, *s*, and gemmae in various stages of development (I–IV). × 85.

Fig. 42. ditto. × 35.

Fig. 43. Mature gemmae, *b* + *c* (× 35) show the point of attachment to the sterigma, *x*. × 70.

Fig. 44. Early stages of germination of gemmae. × 35.

Fig. 45. A, B, Antheridia, external view: A terminal, B lateral. × 175.

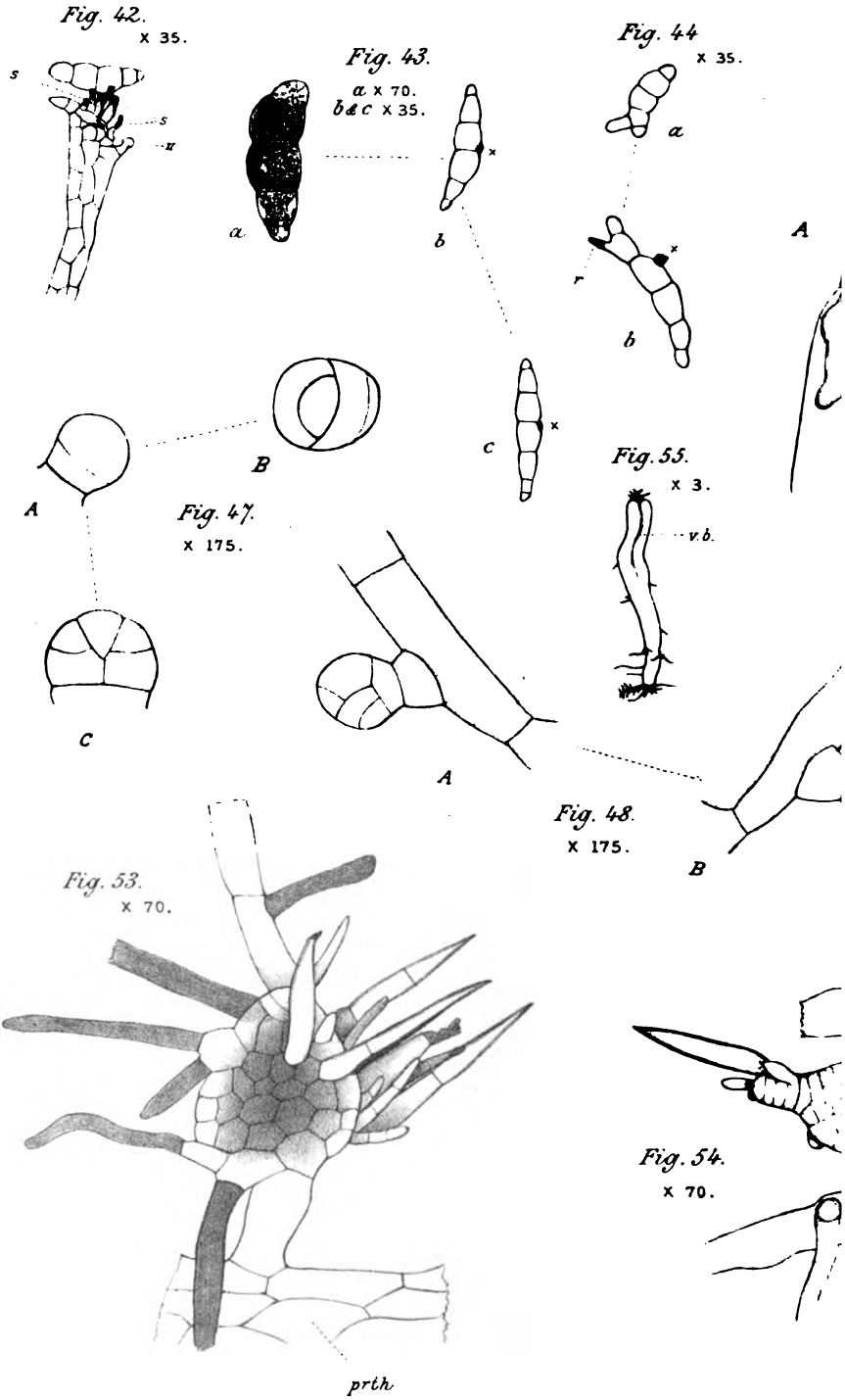


Fig. 42.
x 35.
s
s
x
Fig. 43.
a x 70.
b & c x 35.
a
b
x
Fig. 44
x 35.
a
A
r
x
b
B
A
c
x
Fig. 55.
x 3.
v.b.
Fig. 47.
x 175.
C
A
Fig. 48.
x 175.
B
Fig. 53.
x 70.
prth
Fig. 54.
x 70.

Fig. 45.
x 175.

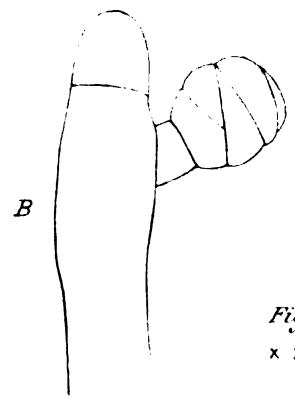


Fig. 46.
x 175.

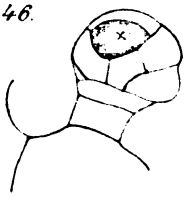


Fig. 49.
x 70.

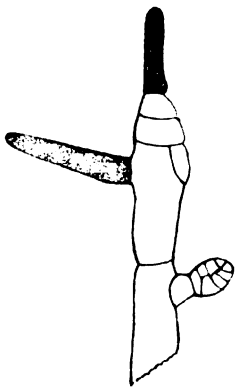


Fig. 50.
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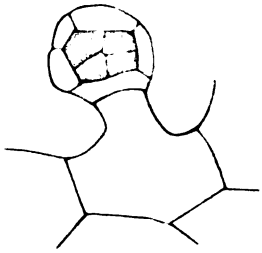
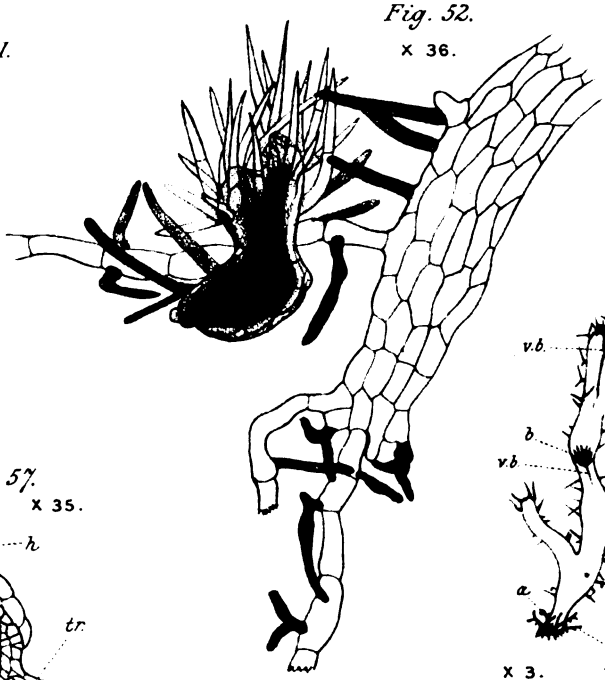
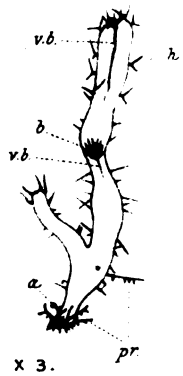


Fig. 51.
x 3.

Fig. 52.
x 36.





x 3.

Fig. 56.

Fig. 57.
x 35.

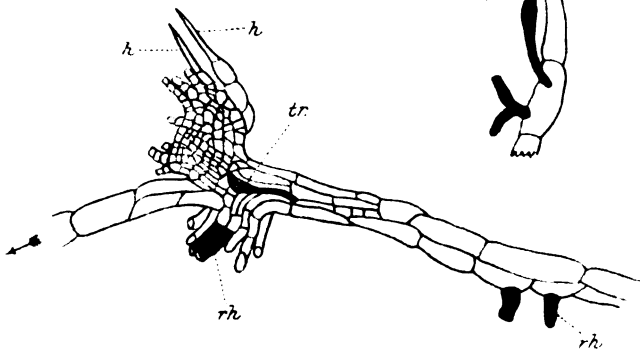


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Fig. 46. Antheridium seen somewhat obliquely from without. *x*, lenticular cell (apical cell?) which has turned brown. × 175.

Fig. 47. A, C, young antheridia in optical section. B, young antheridium seen from above. × 175.

Fig. 48. A, B, young antheridium, external view from opposite sides. × 175.

Fig. 49. Young antheridium, external view. × 70.

Fig. 50. Antheridium in optical section. × 175.

Fig. 51. Flattened prothallus, *pr*, with sterigmata, *st*, at apex: laterally is borne an apogamous sporophyte with first leaf, *l*, root, *r*. × 3.

Fig. 52. An apogamous bud borne on filament growing out from the margin of a flattened prothallus. × 36.

Fig. 53. ditto. × 70.

Fig. 54. Apogamous bud inserted with broad base on the margin of a flattened prothallus. × 70.

Fig. 55. A flattened expansion showing in its lower part the characteristics of a flattened prothallus, but acquiring gradually in its upper part the characters of a sporophytic leaf with median vascular bundle, *v. b.*, and branched conical hairs at the apex. × 3.

Fig. 56. A specimen similar to the above: on the protonema at the base, *pr*, is an antheridium, *a*; rhizoids, *rh*, are formed laterally at the base; towards the apex are the characteristic branched conical hairs, *h*, and the median vascular bundle, *v. b.*, of the sporophyte; on the surface is formed a sporophytic bud, *b*, from which a short vascular strand, *v. b.*, runs down for a short distance towards the base. × 3.

Fig. 57. Longitudinal section through that same bud, showing how the tissue of the bud is continuous with the tissue of the flattened expansion, and how the tracheides, *tr*, of the vascular bundle run from the one to the other. *h*, the characteristic hairs of the sporophyte. × 35.

On the Floating-Roots of Sesbania aculeata, Pers.

BY

D. H. SCOTT, M.A., Ph. D., F.L.S.,

Assistant Professor in Botany at the Normal School of Science, and Royal School of Mines,

ASSISTED BY

HAROLD WAGER.

With Plate XVII.

SEVERAL aquatic members of the natural order Leguminosae are remarkable for a peculiar development of certain of their tissues, leading to the formation of a floating-apparatus, which serves to keep the stem or root, as the case may be, at the surface of the water. In the genera *Aeschynomene* and *Herminiera* it is the secondary wood of the stem which is adapted to this function[1]. In *Neptunia oleracea*, Lour., on the other hand, the floating-tissue owes its origin to the cortex of the stem. This case has been fully investigated by Rosanoff[2], who has shown that the floating-apparatus is here a form of periderm, though differing in almost every respect from ordinary cork. My own observations on this plant have fully confirmed those of Rosanoff. It will be worth while to give a short account of the phenomena in *Neptunia*, as they present many analogies with the case of *Sesbania*, which forms the special subject of this paper.

[1] See De Bary, Comparative Anatomy of the Phanerogams and Ferns, Eng. Ed. p. 500.

[2] Ueber den Bau der Schwimmorgane bei *Desmanthus natans*, Willd., in Bot. Zeitung, 1871. I am indebted to Mr J. G. Baker, F.R.S., of Kew, for information as to the synonyms of this plant. *Desmanthus natans*, Willdenow, is the *Neptunia leracea* of Loureiro, and was originally described by Roxburgh as *Mimosa natans*.

[Annals of Botany, Vol. I. Nos. III and IV. February 1888.]

The floating-tissue of the plant in question forms very conspicuous spongy masses on some of the internodes of the procumbent stem, which is thus enabled to maintain its position on the surface of the water. In Rosanoff's figure 1 (Plate X, l. c.) the tissue is shown at *c* and *d*. The drawing, however, gives but little idea of the very soft, loose texture of the swollen masses. The diameter of the whole body may be nearly an inch, while that of the unswollen parts of the stem is only about $\frac{1}{8}$ of an inch. The length of each mass may be as much as two inches. The external tissue is, in the mature condition, very loosely attached to the stem on which it grows. Humboldt[1] regarded it as extraneous to the plant, and indeed the impression it makes at first sight is quite that of the mycelium of some luxuriant parasitic fungus. The surface is very irregular, showing deep longitudinal furrows. Microscopic examination shows that the tissue consists of very loosely arranged cells, which are greatly elongated, and are sometimes branched. The intercellular spaces are very large, and it is in them only that air is contained. The cells themselves always possess a delicate primordial utricle, a nucleus, and starch-grains; their cavity is at all stages filled with cell-sap, and never contains air. On the inside the floating-tissue passes gradually over into a dense periderm, with its cells in regular radial rows. This is continuous internally with the phellogen. Neither the cell-walls of the floating-tissue itself, nor those of the dense periderm, give the reactions of cork; they consist of unchanged cellulose. In moderately young stems it is easy to trace the remains of the epidermis and of the outermost layers of the primary cortex outside the floating-tissue. Sections through a young internode, when the formation of this tissue is beginning, show that the phellogen arises by division of the third or fourth layer below the epidermis. At first, ordinary periderm is produced all round the stem. The modification of the periderm into floating-tissue begins irregularly at various points of the circumference. At

[1] Cited by Rosanoff, l. c.

this stage the appearance presented is that of a young periderm during the development of the lenticels. In the regions where the production of floating-tissue is beginning, the phellogen is more active than elsewhere, producing more numerous tangential rows of cells towards the exterior. These cells next become rounded, while intercellular spaces appear between them. The cells then rapidly elongate, the epidermis and the two or three outermost layers of the primary cortex are forced outwards, and soon become broken through. The cells of the floating-tissue now successively assume their mature form, growing greatly in length and often branching. Only the ends of the cells and their branches remain in contact. All these changes, which, as we have seen, were at first limited to certain portions of the circumference of the stem, ultimately extend all round it; but in the later stages of growth the irregular furrowed surface of the floating-tissue still bears witness to its originally unequal development. Eventually, towards the end of the period of vegetation, the floating-tissue becomes detached, and the remaining denser part of the periderm acquires suberised walls. Thus a normal cork, of no great thickness, ultimately clothes the surface of those internodes which were before enveloped in the floating-tissue. Those parts of the stem from which this tissue is absent produce from the first an ordinary corky periderm.

The above description is chiefly founded on my own observations, which agree closely with those of Rosanoff. The conclusions which follow from the facts stated are, that the floating-tissue is here morphologically equivalent to the periderm of other Leguminosae, but that it differs from normal periderm in four respects:—(1) The cells do not lose their living contents; (2) their walls do not become suberised; (3) they have large intercellular spaces between them; and (4) it is in these spaces, and not in the cells themselves, that the air is contained.

As already pointed out, the resemblance of the floating-tissue, in its earlier stages, to the complementary tissue of a lenticel, is very striking. Possibly this may be more than

a merely superficial likeness; but further comparative investigation will be necessary before this point can be decided.

Sesbania aculeata, Pers., is a very different plant from the *Mimosa*-like *Neptunia*. *Sesbania* belongs to the papilionaceous tribe Galegeae, and therefore has no near relationship with the plant already dealt with. In spite of this we shall find many points of agreement between them as regards the tissues under consideration.

Sesbania has a tall upright stem, rising high above the water; in this case the floating-tissue is developed in the aquatic roots. In external appearance the tissue much resembles that on the stem of *Neptunia*, forming soft spongy masses as described above. The roots are much branched, and it is only on the relatively main roots that the floating-tissue is formed, the finer lateral branches retaining their normal structure.

The general anatomy of the root is of the usual type; the vascular cylinder is tetrarch, pentarch or hexarch, each phloëm-group having a strand of bast-fibres on the outside, as is so common in the Leguminosae. The pericambium is at first one layer of cells only in thickness, but its cells undergo tangential divisions, beginning opposite the xylem-groups. In the oldest roots examined the pericambium was always three layers at least in thickness. This multiplication of the pericambial layers is a very common phenomenon[1], quite apart from any formation of internal phellogen, with which, as we shall see, the pericambium here has nothing to do. Opposite the xylem-groups the inmost layer of the pericambium is of course used up to complete the cambial ring. Secondary thickening takes place in these roots in the normal manner, as in *Phaseolus* or *Vicia*. The endodermis is distinctly marked, and shows the characteristic structure of its radial walls. The cell-walls of the endodermis ultimately become cuticularised throughout. The primary cortex consists of rounded cells, among which

[1] Cf. Olivier, Appareil tégumentaire des Racines, in Ann. des Sci. Nat. sér. VI, tom. XI.

are very large lacunae filled with air, the structure thus being of the usual aquatic type. It may be added that the larger roots have a persistent parenchymatous pith, while in the smaller lateral roots the groups of primary xylem meet in the middle of the vascular cylinder.

The mature floating-tissue is in most respects similar to that described in *Neptunia*. The cells are much elongated in the radial direction, but as a rule they remain unbranched (see Fig. 4). They are so arranged as to leave large intercellular spaces, containing air, between them. Each cell retains its protoplasm, nucleus, and cell-sap, throughout its existence, and air is never found inside the cells. The walls of the great majority of the cells give the reactions of unaltered cellulose. The tannin-sacs, which occur here, as well as in the primary cortex, form the only exception to this rule; their walls appear to be slightly cuticularised. These tannin-sacs also differ from the other cells of the floating-tissue in their form, which is almost spherical. Their number is insignificant compared to that of the elongated cells, and they may be left out of account in considering the general character of the tissue.

On a superficial examination, the idea suggests itself that the floating-tissue might be formed simply by the elongation of the cells of the primary cortex. Investigation of the development shows, however, that this is not the case. If transverse sections be made of a moderately young root, it is easy to find cases in which some layers of the long-celled floating-tissue are already well developed, while outside them the round-celled lacunar tissue of the primary cortex is still present, though somewhat torn by the extension of the internal structures (see Fig. 3).

The floating-tissue passes over on the inside into a zone of closely-packed cells arranged in regular radial rows, and these again fit accurately into a layer of thin-walled cells, showing recent tangential divisions, and having all the characters of an internal phellogen. Great as is the difference in form between the elongated cells of the mature floating-tissue

and the flat cells of the phellogen, it is easy to find every intermediate stage. In the younger stages the radial rows can be traced outwards from the phellogen far into the floating-tissue; in the mature state the regularity of the radial arrangement is of course less distinct, owing to the displacements which must necessarily be associated with the formation of the intercellular spaces (Fig. 4).

In the oldest roots examined the floating-tissue had become detached, leaving behind the densely-packed cells immediately outside the phellogen. The walls of these cells then become suberised, so that the old root has a corky periderm of the usual character.

The most interesting point which remains to be noticed is the place of origin of the phellogen. In a large proportion of roots with secondary thickening the pericambium, as is well known, is the layer from which the peridermal structures take their rise. To this rule, however, there are many exceptions, as has been especially shown by Olivier (l. c.), who has observed that in a large number of dicotyledonous roots the periderm is external, arising in the outermost living layer of the cortex. In *Sesbania* we have a case different from either of those I have referred to. Sections from the younger roots show clearly that the divisions to which the phellogen owes its origin begin immediately outside the endodermis, in the first or second layer of the primary cortex (Figs. 1 and 2). In some cases both these layers begin to divide (Fig. 1); from comparison with later stages it is probable that in this case the innermost layer alone continues its divisions for any length of time. Careful investigation of roots in every stage of development leaves no doubt that all the peridermal structures arise exclusively from this extra-endodermal phellogen; the pericambium undergoes no further development, beyond the two or three tangential divisions above mentioned, and the endodermis is persistent throughout.

The results attained may be summed up as follows:—

1. The floating-tissue of the roots of *Sesbania* is a secondary cortical structure, arising from a phellogen.

2. This tissue, though thus falling under the definition of periderm, differs from cork in its permanently living cells, its non-suberised cell-walls, and its large intercellular spaces, in which alone air is contained. In all these respects it agrees with the floating-tissue of the stem of *Neptunia*.

3. The phellogen originates *immediately outside* the endodermis, thus differing from the phellogen of most roots with typical periderm.

It may be mentioned that the development of phelloderm, on the inner side of the phellogen, is quite insignificant in amount.

In the light of recent investigations on roots as organs of respiration[1] it seems not improbable that one function of the floating-tissue may be to facilitate the supply of oxygen to the organs on which it occurs. This tissue would then present an analogy with lenticels—a point not without interest, considering the similarity, above noticed, in the development of the two organs.

It has long been known that some species of the genus *Jussiaea* also possess modified roots, which serve as floats, and develop a special floating-tissue. The existing investigations tend to show that this tissue here forms part of the primary cortex, but a renewed investigation of these plants seems desirable[2].

I have to thank Mr. Thiselton Dyer, Director of the Royal Gardens, Kew, both for first calling my attention to the plants investigated, and also for the supply of material.

[1] Goebel, Über die Luftwurzeln von Sonneratia, in Berichte d. Deutschen Bot. Gesellschaft, Bd. IV, Heft 6, July, 1886. Ludwig Jost, Ein Beitrag z. Kenntniss der Athmungsorgane der Pflanzen, in Bot. Zeitung, 1887. p. 601.

[2] Martins, Sur les racines aérifères des espèces aquatiques de Jussiaea, in Mém. Acad. de Montpellier, Tom. VI (1866).

EXPLANATION OF FIGURES IN PLATE XVII.

Illustrating Dr. D. H. Scott's and Mr. H. Wager's paper on the Floating-Roots of *Sesbania aculeata*, Pers.

Fig. 1. Portion of a transverse section of a young root, showing the first divisions of the inner cortical cells to form the phellogen. *l*, primary lacunar tissue of cortex. *ph*, phellogen. *e*, endodermis. *pc*, pericambium. *ph. f*, bast-fibres of a phloëm group. × 360. The shaded cells in the cortex are tannin-sacs.

Fig. 2. Similar section from a much older root. The phellogen is now in full activity. *fl*, youngest part of floating tissue. *t*, tannin-sac. Other letters as before. × 360.

Fig. 3. Transverse section of a young tetrarch root. One or two layers of the floating tissue have already been formed. The torn primary cortex is shown outside the floating tissue. Letters as before. × 120.

Fig. 4. Section of an old root, showing a portion of the floating tissue in position. Letters as before. × 200.

Fig. 1.

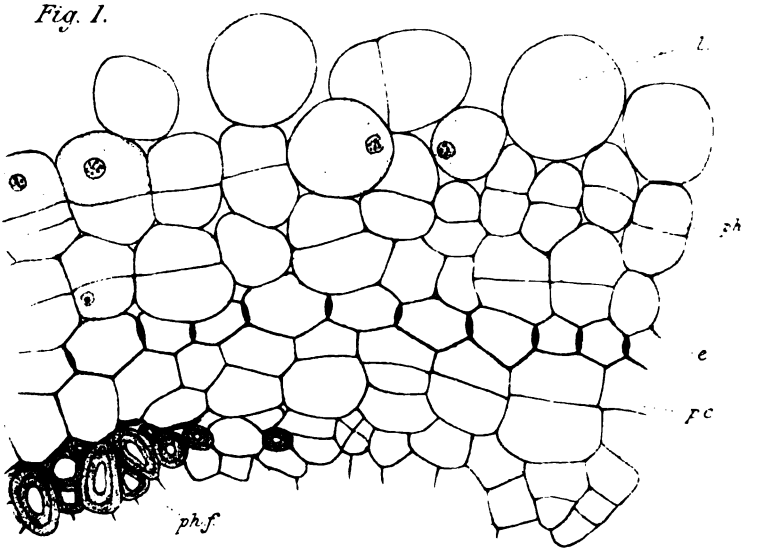
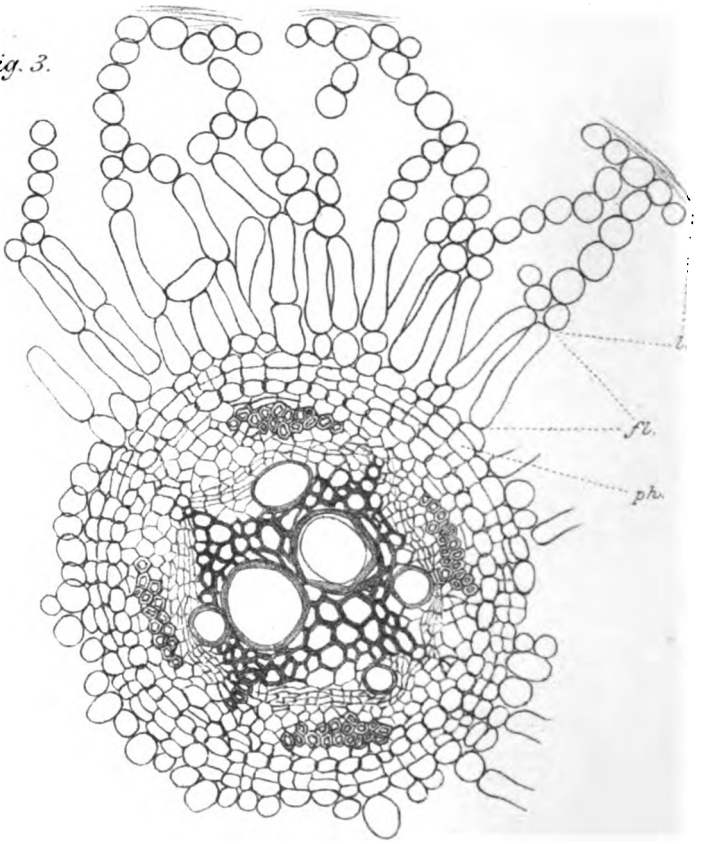


Fig. 3.



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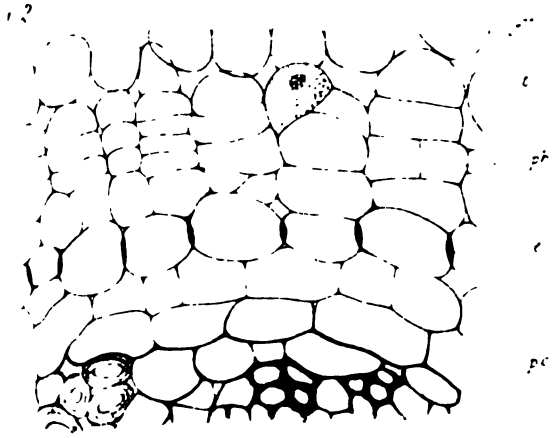

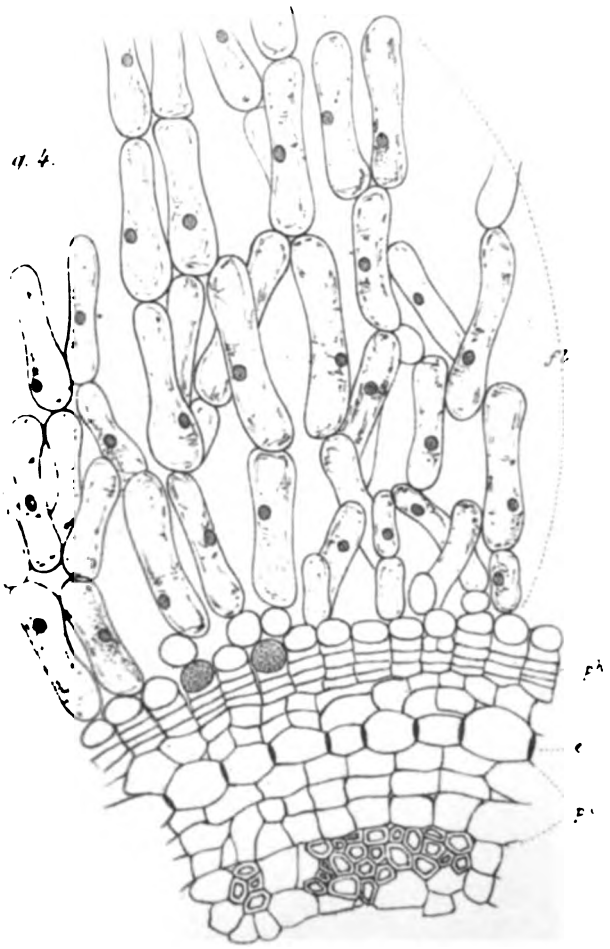

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Fig.

On some Anomalous Cells developed within the interior of the Vascular and Cellular Tissues of the Fossil Plants of the Coal-Measures.

BY

WILLIAM CRAWFORD WILLIAMSON, LL.D., F.R.S.,

Professor of Botany in the Owens College and in the Victoria University.

With Plate XVIII.

IN the eighth of my series of memoirs 'On the Organisation of the Fossil Plants of the Coal-measures[1],' I described the vascular axis of a Fern, *Rachiopteris corrugata*, Will., the vessels of which were filled with cells apparently identical with the thylosis found in some living plants. In Part x of the same series[2] I subsequently described the petiole of another Fern, *Rachiopteris insignis*, Will., the vessels of the fibro-vascular bundle of which were filled with cells of a similar kind. In Part ix. of the same series[3] I further described a number of Lycopodiaceous macrospores, the interiors of many of which were occupied by some remarkable accumulations of cells of various sizes and arranged in diversified ways. During the last ten years there have accumulated in my cabinets various other examples of parasitic or saprophytic cells, lodged within the tissues of fossil plants, revealing a condition of things existing at the Carboniferous epoch not undeserving the attention of botanists. In most of these instances what may for the sake of distinction be recognised as the *intrusive* cells are lodged

[1] Phil. Trans., vol. 167, Part i. p. 214, Pl. 6, Figs. 15, 16.
[2] Phil. Trans., Part ii. 1880, p. 506, Pl. 16, Figs. 19–20, and 21.
[3] Phil. Trans., Part ii, 1878, p. 345, Pl. 23, Figs. 65, 66, 66 A, 66 B.

[Annals of Botany, Vol. II. Nos. III and IV. February 1888.]

within the interior of *host*-cells, which latter almost always belong to the cortex of the invaded plant. In a smaller number of instances the hosts are the vessels or tracheids of fibro-vascular bundles. It is somewhat more than probable that these two types of hosts, the cellular and the vascular, may have sheltered two distinct types of organism.

Fig. 1 represents a fragment of the bark of some unknown plant from the productive Halifax beds. It consists of cells variable in size and form, which in the figure are enlarged 124 diameters. Considerably more than the half of these cells are more or less filled with smaller cells, which vary greatly in size as well as in the way in which they are grouped. Thus at *a* we have one solitary spherical cell $\frac{1}{600}$ of an inch in diameter. At the lower part of the host-cell, *b*, we have a group of cells similar to *a*, the remainder of the host being empty. At *c* we have a host-cell packed with intrusive cells of various sizes; at the upper and lower parts of the cavity these cells approximate to about $\frac{1}{300}$ (all these measurements are given in fractional parts of an inch) in diameter; but those occupying its centre are much smaller, averaging about $\frac{1}{1800}$. At *d* a host-cell has its cavity densely filled with very small cells, approximating to a mean diameter of $\frac{1}{3600}$; whilst in another host-cell belonging to the same fragment of bark, but not included in the figure, the intrusive cells average even less than $\frac{1}{7000}$ in diameter.

We thus see that in the fragment from which Fig. 1 is taken, numerous host-cells are filled with intrusive ones of every size intermediate between $\frac{1}{600}$ and $\frac{1}{7000}$; yet their aspects, and the way in which they are aggregated, indicate that whatever may be their nature, they represent varied conditions of some common vegetable organism. Whenever free from contact with one another they are perfectly spherical, whatever their dimensions; but they frequently form small clustered groups when, mutually compressing one another, they exhibit the familiar aspects of parenchymatous tissue.

Fig. 2 is a single host-cell from the same specimen as Fig. 1, enlarged to 262 diameters. It illustrates several

conditions of common occurrence amongst these objects. At *a*, *a*, we have some isolated spherical cells. At *b*, *b*, are similar ones, but of much smaller dimensions. At *c* is an oval cluster of a form that is not uncommon. It looks like a group of cells, of various sizes, enclosed either within a mother-cell or within some viscid substance that binds the cluster together in a defined manner. At *d* is a somewhat less defined but otherwise similar cluster, though of larger size.

Fig. 3 is another host-cell from the same fragment of bark, but in which all the contained cells retain their spherical form.

Fig. 4 is a host-cell from another fragment of bark; in its centre is a single free spherical cell, whilst numerous others exhibit a tendency to adhere to the hostal cell-wall. At the lower end of the host a cluster of cells cohere, forming a small parenchymatous mass.

Fig. 5 is a host-cell from a transverse section of a stem or rhizome of the type of the genus *Anachoropteris* of Corda, but which is giving off a petiolar branch, apparently identical with my *Rachiopteris insignis*[1]. Many of the cells of the inner layer of the cortex of the *Anachoropteris* are in a condition very similar to those of Fig. 1. Fig. 6 represents one of these host-cells, in which we have two clusters of intrusive cells, *a* and *b*. At *c* one of the cells of the group *b* is filled with a cluster of daughter-cells. Innumerable figures might be drawn from the above section showing various shapes, sizes, and grouping of its intrusive cells; reference will be made to the vessels of this specimen later on.

Figs. 6, 7, and 8 are three free cells from another parenchymatous fragment, which respectively contain one, two, and four free spherical intrusive cells. Fig. 9 is a host-cell from the *outer* bark of a section of *Lyginodendron Oldhamianum*, isolated cells of which contain intrusive cells in very varied conditions of size and grouping. These host-cells are few in number compared with those of the cortex which are entirely empty.

[1] Memoir x. Phil. Trans. Part ii. 1880, p. 507.

This Fig. 9 presents a single cluster of closely adherent cells, reminding us of those seen at Fig. 2, *c*.

Fig. 10 is a host-cell from the outer bark of another example of *Lyginodendron Oldhamianum*, in which single host-cells are isolated as in Fig. 9. In this specimen, as in some others, the intrusive cells are very irregular in size and form, whilst the spaces within the host which the cells do not occupy are filled with a dark brown carbonaceous substance that has somewhat the appearance of having once been in a fluid or semi-fluid state. There is evidently some connection between the presence of this dark substance and that of the intrusive cells, since the former is very rarely found in the cells of the cortex in which intrusive cells are not present. The above observations apply equally to the bark from which Fig. 9 was taken.

I have thus far limited my descriptions to specimens in which the intrusive cells occur in various examples of parenchyma, chiefly cortical. But my cabinets contain several examples in which the interiors of scalariform vessels or tracheids are occupied by cells. In previous memoirs I have described two such cases. The first was in Memoir viii, where I dealt with my *Rachiopteris corrugata*[1], and the second in Memoir x[2]. Since these descriptions were published I have met with a third example in which similar cells occur in the vessels of the inner or non-exogenous zone ('*étui medullaire*' of Brongniart), of a yet undescribed species of *Lepidodendron*.

Fig. 11 represents two of the smaller vessels of the vascular bundles of *Rachiopteris insignis*, as seen in a transverse section of that petiole, and Fig. 12 is part of a longitudinal section of a larger vessel from the same bundle. Each of these figures is enlarged 200 diameters. The contained cells fill the entire interior of each of these vessels.

Fig. 13 is a transverse section of two similar vessels, and Fig. 14 a longitudinal one of a single vessel, from the inner

[1] Phil. Trans. vol. 161, Part i. p. 214, Pl. 6, Figs. 15, 16.
[2] Phil. Trans. Part ii. 1880, p. 506, Pl. 16, Figs. 20, 21.

vascular cylinder of the *Lepidodendron* referred to above. In the latter example the cells are less densely packed within the vessels than in the former one; hence they retain more of their primitive spherical form.

In my memoir ix[1], I figured and described a selection from a very large number of macrospores belonging to a species of Lycopodiaceous strobilus, and the endosporal cavities of these spores are more or less filled with cells of various sizes and conditions. In many instances these cells are free; in others they are combined into a parenchymatous tissue. In most of the examples the cells are seen to be located within an inner membrane, *c*, which I assume is the endosporal membrane lining the very thick exosporium. Two of these macrospores are represented in Figs. 15 and 16, the former being enlarged 570 diameters, and the latter 250 diameters. The thick exosporium, *a*, of these spores is always clothed externally by numerous simple or branched hair-like appendages, *b*. Both the above examples contain numerous cells, the two specimens representing sufficiently closely the two extremes of the average sizes to which these cells attain. Those of Fig. 15 have a mean diameter of about $\frac{1}{800}$ of an inch. In Fig. 16 two or three, as at *c*, are larger than the rest, being $\frac{1}{800}$ in diameter, but most of the cells in this specimen have a maximum diameter of about $\frac{1}{1800}$ of an inch.

In my memoir x[2], I represented similar cells in the interior of the spores to which, in a previous memoir, I gave the provisional name of Zygosporites, and in Plate 18, Figs. 42 and 45 of the same memoir, similar cells were shown, occupying the macrospores of my *Strobilus Traquairia*. In Plate 17, Figs. 25 and 31 (loc. cit.), similar cells are seen in several species of the curious reproductive bodies, belonging to some, as yet, unknown plants, and to which bodies I have assigned the provisional name of *Sporocarpan*. I have not thought it necessary to reproduce all these anomalous forms in the present memoir. These aspects are approximately represented

[1] Phil. Trans. Part ii. p. 345 *et seq.*, Pl. 23, Figs. 65, 66, 66 A, 66 B, 66 C.
[2] Phil. Trans. Part ii. 1880, Pl. 19, Fig. 55.

in the two macrospores, Figs. 15 and 16, though I am far from concluding that all these various examples of contained cells are homologous.

The question remains, what are these intrusive cells? So far as Figs. 11, 12, 13 and 14 are concerned, I think we shall not risk making any great mistake in concluding that we have in them genuine examples of the so-called thylosis. The structures so named vary in different examples, but it appears to me that the specimens now described approximate sufficiently closely to the general type of thylosis to be legitimately recognised as examples of it. But it is otherwise with the forms represented in Figs. 1–9, where the intrusive cells are included, not within vessels, but within various modifications of parenchymatous tissue. The most conspicuous feature presented by these intrusive cells is the great differences in their sizes, as well as in the modes in which they are aggregated, even within the same host-cell. These differences are so great as to suggest, at the first glance, that we have more than one kind of object even within one host-cell. But opposing this conclusion is the fact that varied as are the forms, sizes, and groupings of these intrusive cells, we find every possible gradation between even the most distinct varieties; hence I conclude that whatever these objects may be, they all belong to one type of vegetable organism. At the same time we cannot identify them with any of the thylosis. If the description of the origin and development of these thylosis[1], given by Max Reess, be correct, they can only find their way into the interiors of elementary tissues whose walls are furnished with points that are weak because of their thinness. The vessels represented in Figs. 11–14 were so far scalariform as to present such areas of weakness, rendering it at least possible that the cells which they contain *may* be thylosis. But the walls of the parenchymatous cells which contain the intrusive ones now figured, exhibit no indications whatever of having had any such thin

[1] See Professor M. Ward's English Translation of Sachs' Physiology of Plants, p. 581.

spots; hence we cannot apply Reess' explanation to their origin and nature.

The question, may these objects have a fungoid character, suggests itself. Of all the hundreds of host-cells that I have examined no one has contained the slightest trace of a hyphal filament, hence the presumption against the fungoid idea is a strong one. Assuming the accuracy of this reasoning, and yet remembering that the objects in question must have had some sort of an origin, the question arises can these cells be algoid ones? In the second edition of the English translation of Sachs' Text-book of Botany, we have at p. 247 some remarks that may bear upon the question. After referring to the fact that colonies of *Nostoc* have long been known to exist within the cavities of cryptogamic plants, in some of which cases the germs developed into round balls, the author adds, 'The entrance of *Nostoc* into the parenchyma of a dicotyledonous plant, *Gunnera*, is brought about, according to Reinke, in a different manner; the deeper lying cells of the outer part of the stem, themselves covered by layers of parenchyma, are densely filled with colonies of the Alga.' Now if the germs of a *Nostoc* could thus find their way into the deeper layers of a cortical tissue, there is no reason why another and lower unicellular Alga should not be able to do the same. Whether or not this is the true explanation, the fact that during the Carboniferous age some unicellular vegetable organisms did find their way even into the deeper cortical tissues of various plants of high organisation is certainly true, and the instance of the *Gunnera* appears to present the nearest approach that living plants have hitherto supplied to what has occurred in the Carboniferous ones.

But the still more curious cases of the macrospores, like Figs. 14 and 15, remain for consideration. When recording these instances in my memoir referred to above, I was strongly inclined to believe that what I then spoke of as endosporal cells were normal developments from an endosporal protoplasm. And I am still far from certain that this idea is not a true one. At the same time the absence of all similar

growths from the macrospores of living Selaginelleae affords a strong argument against such a conclusion. When I showed my specimens to my friend, Hermann Graf zu Solms-Laubach, of Göttingen, he at once concluded that the intrusive cells were either parasitic or saprophytic. On a later day I also showed them to Professor de Bary, of Strassburg, but, whilst recognising their existence as an indisputable morphological fact, he, with his wonted philosophic caution, hesitated to pronounce any opinion as to their nature. Under these circumstances it would be presumptuous for me to pronounce dogmatically when so high an authority shrinks from doing so. Nevertheless the facts appear to be sufficiently interesting to be put on record, hoping that research may some day throw a more definite light on the explanation of them.

THE OWENS COLLEGE BOTANICAL LABORATORY,
January 9, 1888.

EXPLANATION OF FIGURES IN PLATE XVIII.

Illustrating Professor Williamson's paper on some Anomalous Cells developed within the tissues of the Fossil Plants of the Coal-Measures.

Note. The cabinet number appended to each description is that of the specimen in my collection from which the figure was taken. W. C. W.

Fig. 1. Fragment of parenchymatous bark, most of the cells of which contain intrusive cells. × 124. Cabinet number, 1638.

Fig. 2. A single cell from the same specimen as Fig. 1. × 262. Cabinet number, 1638.

Fig. 3. Another cell from the specimen Fig. 1. × 262. Cabinet number, 1638.

Fig. 4. A single cell from another bark-fragment. × 400. Cabinet number, 1639.

Fig. 5. A cell from the bark of a transverse section of a stem of *Rachiopteris corrugata*, Will. × 400. Cabinet number, 264.

Figs. 6-8. Three cells from a parenchymatous fragment. × 400. Cabinet number, 1642.

Fig. 9. Single cell from the outer bark of a transverse section of a stem of *Lyginodendron Oldhamianum*. × 400. Cabinet number, 1640.

Fig. 10. Single cell from a tangential section of the outer bark of another specimen of *Lyginodendron Oldhamianum*. × 400. Cabinet number, 1146.

Fig. 1.

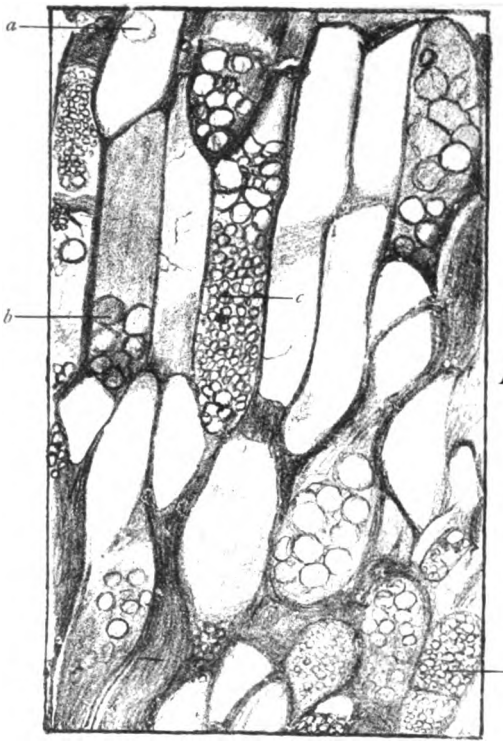


Fig. 9.

Fig. 6

Fig. 8.

Fig. 7.

Fig. 16.

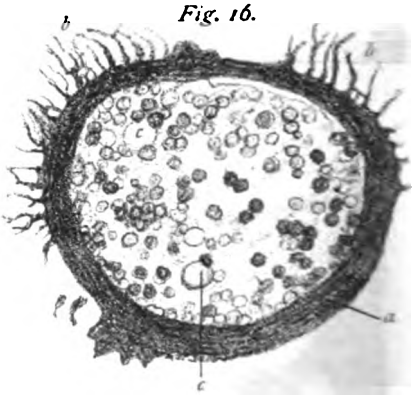


Fig. 2.

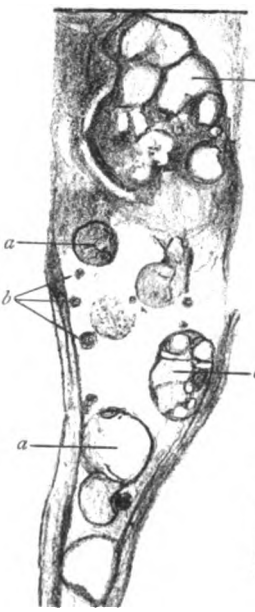
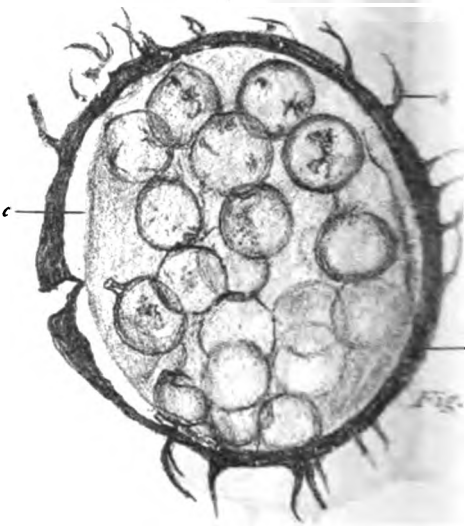


Fig. 3.



W. C. Williamson, del.

WILLIAMSON.—ON ANOMALOUS CELLS IN FOSSIL PLANTS.

Fig. 12.

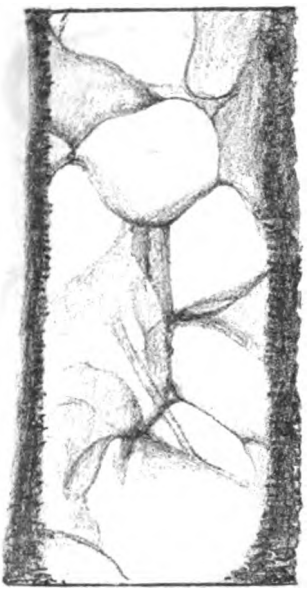


Fig. 14.

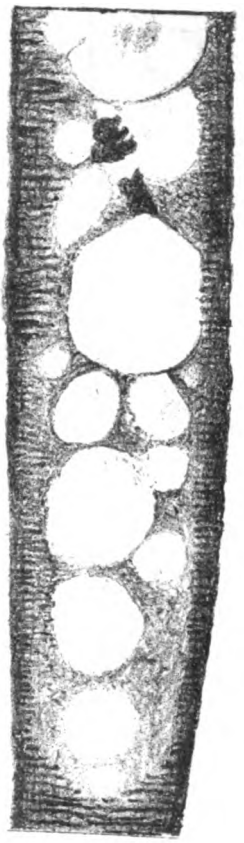


Fig. 11.

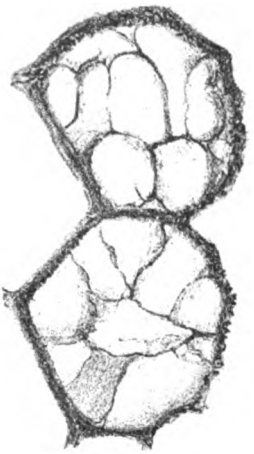


Fig. 4.

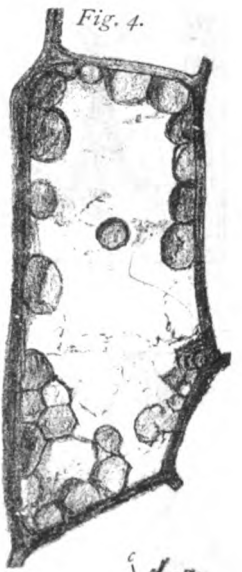
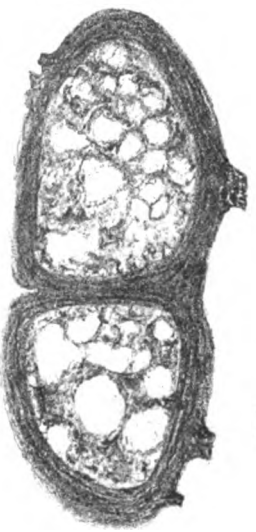


Fig. 10.

Fig. 13.



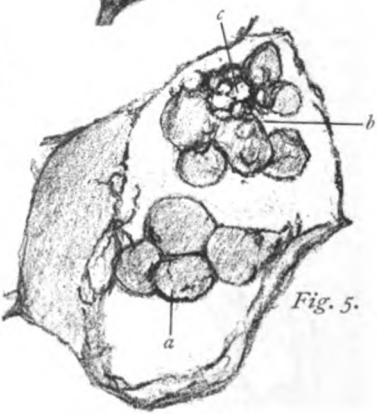


Fig. 5.

University Press, Oxford.

Fig. 11. Two small vessels from the vascular bundle of a transverse section of the petiole *Rachiopteris insignis*, Will. × 600. Cabinet number, 265.

Fig. 12. Longitudinal section of part of a vessel of the vascular axis of an oblique section of a petiole of *Rachiopteris insignis*. × 200. Cabinet number, 265.

Fig. 13. Two vessels from a transverse section of a stem of the inner vascular cylinder of a small undescribed form of *Lepidodendron*. × 200. Cabinet number, 418.

Fig. 14. Part of a vessel from a longitudinal section of the specimen Fig. 13. × 200. Cabinet number, 419.

Fig. 15. A Lepidodendroid macrospore. × 570. Cabinet number, 610.

Fig. 16. A macrospore of the same type as Fig. 15, but containing very small cells. × 120. Cabinet number, 612.

Some recent Publications bearing on the question of the Sources of Nitrogen in Plants.

BY

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IN the *Berichte der deutschen botanischen Gesellschaft* for 1885[1] there appeared a paper by Professor Frank of Berlin, entitled '*Ueber die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze*,' in which the author made known to science the results of some investigations of a kind sufficiently astonishing at the time, and which have been considered of late as possibly leading to yet more remarkable results when they are further examined. I propose to give a brief account of the published substance of this and certain other papers, with short critical notes of the views which the facts have suggested.

In the above paper Frank states that researches were being made in order to obtain information as to the culture of Truffles, which have long been known to affect the neighbourhood of living beeches, hornbeams, and oaks. Having regard to the observation[2] that the Truffle-like fungus *Elaphomyces* has its mycelium affixed to the roots of living pines, like a parasite, the question arose whether the true Truffles may not also be parasitic on roots?

[1] pp. 128–144, Pl. x.

[2] Reess, 'Sitzungsber. d. physik-med. Soc. zu Erlangen, 10 May, 1880.'

[Annals of Botany, Vol. I. Nos. III and IV. February 1888.]

Investigation yielded the unexpected result that certain trees, especially the Cupuliferae, have almost the whole of their root-system covered with mycelium, the fungus being associated symbiotically with the root: the conclusion is drawn that the fungus-hyphae act the part of the root-hairs elsewhere, and that the whole of the absorption from the soil is due to their action.

The younger roots of any oak, beech, hornbeam, hazel, or chestnut, at any time of the life of the tree, from any of the distant places examined, were found to consist of a double structure—the true root as a sort of core, covered by a close web of mycelium as an envelope. Such an association of root and fungus is to be named a *Mycorhiza*.

In appearance the Mycorhiza resembles some sclerotia, the mycelium forming a sort of pseudo-parenchyma, the outer walls of which become dark brown as it ages. The weft of mycelium covers the root-apex as well as the parts behind, and is at first white: even the root-cap is therefore covered in.

The coating of mycelium varies in thickness, but usually forms a layer several cells deep. Hyphae dip down between the cells of the outer layer of the root proper, and grow around them completely; they do not leave the cell-walls, however, and are not found in the cell-lumina, nor deeper down in the tissues of the root. These 'endophytic hyphae' are very much thinner than those outside.

The outer surface of the mycelial envelope may be clean and smooth, and it will be understood that so complete and continuous a covering prevents the formation or emergence of root-hairs; in many cases, however, free hyphae develope from the outer surface of the mycelial envelope, and radiate out into the soil, growing at their ends, and curiously resembling true root-hairs in many morphological points.

Frank insists moreover that they replace the root-hairs physiologically. They become attached to particles of soil, and can be the only means for absorbing water and substances dissolved in it. Sometimes many of these free hyphae

grow out into the soil parallel to one another, and form compound strands in every essential respect like the *Rhizomorphs* (of *Agaricus melleus* for instance); from such strands free hyphae may radiate out into the soil in their turn again. Anastomoses and ramifications of the most varied kind may take place in the surrounding soil, and the regions where Truffles grow have the soil permeated with such systems.

From the study of longitudinal sections, &c., Frank concludes that the development of the Mycorhiza is somewhat as follows. Since the mycelium closely invests the whole root-tip, it must elongate coincidently with the root: as matter of fact the hyphae covering the root-cap are thinner, and show every sign of growth, both by elongation of the existing hyphae, and by the interpolation of new branches between those already formed. The 'endophytic hyphae' do not develope until the growing apex has passed out of the stage of elongation; hence no organic connection between fungus and root is formed at the apex. The complete covering of the apex seems to be causally connected with the very feeble development of root-cap cells—in other respects the root (that of *Carpinus* is figured) conforms to the common type for Dicotyledons; probably, on the one hand, the pressure prevents the fuller development of root-cap cells, and, on the other, the fungus-web has acquired the protective function of a true root-cap.

Although the first stages of germination of the tree are passed through without the appearance of the fungus on the radicle, the lateral rootlets are usually soon attacked. The hornbeam is attacked very early, the young oak may remain a year or two free from mycelium.

In contrast to the roots of plants cultivated without the fungus, the Mycorhiza is shorter and thicker—the number of layers in the plerome and periblem increase: the tendency to branch is also increased, and the lateral roots emerge at points closer together, on account of the slow growth in length. These peculiarities give the Mycorhiza a 'coral-like' shape. As regards endogenous origin, monopodial

order of development, &c. of the lateral roots the My behaves like an ordinary root; but of course the e young root is covered by mycelium from the first.

Further back, on older parts of the roots, the m turns black and dies off: its life coincides with the of the younger parts, and may be longer or shorter ac to circumstances.

Sufficient has been said as to the ubiquity of the and its presence at all ages on all Cupuliferae. The My is (in beech and hornbeam) most abundant in the parts of the soil, among the vegetable remains; the are also most abundant there, and Frank states t ripe Truffles rest on and in a dense matting of My As the roots go deeper, the Mycorhiza is rarer: quite in accordance with the known fact that the *Saug* —*i. e.* young active lateral roots—are more sparsely de on deeper roots, and the author's point is made on that when they are found low down they are in t of Mycorhiza. The assumption is that the growi carries mycelium down with it.

It is not superfluous to mention that numerous othe growing in woods were examined, herbs, shrubs, an but birches, ashes, alders, elms, &c., &c. were all d the fungus. The Mycorhiza is so far a special pecul the Cupuliferae.

Subsequently, Frank states that he has found a My here and there on species of *Salix* and *Populus*; a on pines, spruces, and firs in the neighbourhood of This is noted as remarkable because *Elaphomyces* known in the places examined—it will be remembe Reess had found it on pines.

Frank then discusses the probability of the fungus been seen by others, and comes to the conclusi Gibelli[1] has mistaken it for a disease-producing p R. Hartig's *Rosellinia* (*Rhizoctonia*) *quercina*[2] is a

[1] 'Nuovo studi sulla malattia del Castagno detta dell'inchiostro.' Bol
[2] 'Unters. aus d. forstbotanischen Inst. zur München,' 1880, p. 1.

different fungus. The reason Frank's fungus has been overlooked is probably that those who investigate roots use the seedlings, water-cultures, &c.

Beeches, hornbeams, oaks, and hazels, removed from the ground in spring, when one to two years old, and already bearing Mycorhiza, can be easily grown as water-cultures, with the result that the roots go on growing free from the fungus—or, rather, that new laterals are formed as water-roots, and the mycelium does not spread on to these. The fungus could not be cultivated.

As to the question, what is the systematic position of the fungus? no clear answer can be given. It is no doubt the mycelium of a subterranean form—one of the Tuberaceae or Gasteromycetes, perhaps. But new forms are discovered every day, and the presence of a mycelium does not necessarily imply the presence of the perfect fungus fructification; mycelia may go on growing and sterile for years.

We now come to Frank's views as to the biological significance of the Mycorhiza. The organic union between root and mycelium, their harmonious growth, and the close physiological relations which must exist between them, all point to this being a new case of symbiosis. From the side of the root, we must regard the fungus as a parasite, which takes from the former food-supplies of the nature of carbonaceous assimilated material: its minerals &c. must be taken by the fungus itself from the soil, the free hyphae acting like root-hairs. We may regard the thickening and other changes produced in the root as similar to the alterations met with in hypertrophy, &c.,—here in a slight degree only—due to a stimulus exerted by the parasite on the host. The roots are by no means killed, however, and that they preserve their capacity to serve the tree is proved by the well-being of the latter. We must conclude that the root-fungus, in the mycelium stage at least, is not injurious to the root and tree.

Under such conditions we must look for a contrary benefit derived from the fungus by the tree, and Frank sees this

in the functioning of the mycelium as root-hairs. Since the whole surface of the root is covered by the mycelium, water and dissolved substances can only reach the former through the latter, and the extensive ramifications of the outlying mycelial strands and hyphae in the soil no doubt achieve the work of true root-hairs. Frank also sees in the enlargement of the epidermis-cells of the root and their enclosure in fine hyphae an adaptation which probably works to the same end. We are therefore to look upon the root-fungus as the sole organ for the absorption of water and materials from the soil, in the cases concerned. Frank therefore contrasts the mode of nutrition of Cupuliferae, as *heterotrophy*, with that of ordinary land plants—*autotrophy*.

The comparison with the symbiosis of Lichens is evident, and it need only be remarked that just as the gonidia of a Lichen are not incapable of independent existence, so the roots of oaks, beeches, and other Cupuliferae may be grown independently for years in water-culture.

Whether the Cupuliferae can develope under ordinary conditions, with their roots in the soil, in the absence of the 'nurse fungus,' and whether they would do better or worse simply cannot be decided, because there appear to be no Cupuliferae free from the fungus.

Just as Lichen-fungi will not flourish without the host Alga, so the root-fungus seems to be dependent on the tree: no efforts to cultivate the mycelium artificially have succeeded.

Such is, shortly abstracted, the story of the Mycorhiza as told by Frank in the first instance.

This was soon followed by two more or less critical notes, first by Woronin[1], and then by O. Penzig[2]. Woronin writes to the effect that he had known the 'Mycorhiza' for two years, having found it in Finland when investigating the biology of certain edible *Boleti*, &c.

[1] Ber. d. deutsch. Bot. Ges., 1885, p. 205.

[2] Ibid. p. 301.

Woronin's Mycorhiza was found on species of *Salix* and *Populus*, and on Conifers, *Corylus*, and a few other plants. Since Truffles 'do not exist in Finland,' the mycelium in question cannot belong to that fungus, but Woronin thinks it not improbable that a *Boletus* is here concerned.

Woronin then goes on to remark that Kamienski had already discovered the symbiosis of which Frank makes so much, in 1882, in a work on *Monotropa Hypopitys*[1], pointing out the same thing in *Fagus sylvatica* and the Coniferae, whence the priority belongs to this observer.

The note by O. Penzig has reference to Frank's remarks about Gibelli's study of the chestnut-disease, and may be taken as admitting generally the possibility of Frank's conclusions, though protesting against some details which do not concern us at present.

M. Reess also adds a few notes on the subject of *Elaphomyces* and other root-fungi[2], and he too points out that Kamienski's paper contains the germ of the matter. Reess states that the hyphae of *Elaphomyces* not only enter between the outer cortical cells of the pine-root, but drive the cell-wall before them as vesicles into the lumina. As regards common growth, distribution, occurrence, &c. of the mycelium on the roots, Reess states that the anatomical and other facts concerning *Elaphomyces* and pine-roots accord with Frank's facts about the Mycorhiza of Cupuliferae.

Reess also states that he has repeatedly seen fungus-envelopes on the roots of other plants as well as the pine. He has also investigated Kamienski's fungus on *Monotropa*, and finds his observations in some points differing from those of that observer: he believes the *Monotropa*-fungus to be different from *Elaphomyces*, but cannot be sure. Reess admits that these and Frank's root-fungi must take nutriment from the roots; but regards the rest of the conclusions as needing much more careful investigation.

The above criticisms are replied to by Frank in an article

[1] Mem. de la Soc. Nat. des Sc. Nat. et Math. de Cherbourg, T. xxiv.

[2] Ber. d. deutsch. bot. Gesellsch. 1885, p. 293.

in the *Berichte der deutsch. bot. Gesell.* for Nov. 19, 1885[1], in which he insists on his claims to have 'discovered a hitherto unknown biological phenomenon in the nutrition of certain trees,' &c. &c. He points out that Woronin's rejoinder as to Kamienski's having already discovered the nature of the Mycorhiza is premature, since Kamienski only discovered mycelium investing the roots and denied the organic union of root and fungus. However, it seems unnecessary to enter into a criticism of the discussion as to priority, as it may be accepted that Frank was clearly the first to generalise, and to suggest in the wide sense the biological significance of the symbiosis.

What is more important is that Frank himself investigated the *Monotropa* roots anew, and found facts beyond the mere association of fungus and roots described. He discovered that the hyphae of the fungus are not simply on the surface of the *Monotropa* root[2], but enter between the cells: this, as in the case of the Cupuliferae, only takes place on those parts of the root behind the region of growth in length. Hence the Mycorhiza of *Monotropa* is, like that of the Cupuliferae, a case of organic union and symbiosis between the fungus and the root.

Frank then proceeds to state:—

(1) That the phenomenon which he at first thought confined to the Cupuliferae and a very few other trees probably appertains to 'all trees under certain conditions.' He finds a form of Mycorhiza on the roots of the Scotch pine, the Weymouth pine, the spruce, the silver fir, the larch; also in Salicineae, alders, and birches, and in one case even on the lime, and *Prunus spinosa*.

(2) That 'the Mycorhiza is formed only in a soil which contains humous constituents or undecomposed vegetable remains; the development of Mycorhiza increases or di-

[1] Neue Mittheilungen uber die Mycorhiza der Bäume und der Monotropa hypopitys, pp. xxvii–xxxiii.

[2] In a foot-note Frank states that he has found a case of this kind on *Andromeda polifolia*.

minishes with the poverty or richness in these constituents.'

(3) 'The fungus of the Mycorhiza conveys to the tree not only the necessary water and the mineral nutritive substances of the soil, but also organic matters taken direct from the humous and decomposing vegetable remains.' Only by the mediation of the fungus is the tree enabled to employ directly such organic matters.

(4) The theory, superseded in the doctrine of the nutrition of plants, of the direct nutrition of green plants by humus, is therefore again brought to the front in the light of the Mycorhiza, although in another sense than formerly, and the significance of the humus and the covering of dead leaves on the soil needs further investigation and consideration.

This is the substance of Frank's renewed and extended theoretical statements. They speak for themselves; and it must be admitted that he proposes to raise a very large superstructure on the foundation of his anatomical investigations, and that, in doing so, he assumes a proportionately heavy responsibility.

The next important communication on the subject is again by Frank, in the *Berichte der deutschen botanischen Gesellschaft* for 1887[1]. In this he expressly sums up once more the chief points already insisted upon, and then proceeds to add other facts.

He finds a peculiar formation of pigment associated with some kinds of Mycorhiza, reminding us of the pigments formed by certain Schizomycetes and Saccharomycetes, and not unknown in connection with higher fungi (no cases of the latter are cited, but the author would no doubt accept the green dye in wood affected by *Peziza aeruginosa* as an example). These pigments stain the membranes and contents of the fungus hyphae as well as the surrounding media.

Frank then proposes to classify all the known forms of Mycorhiza as follows:—

[1] Ueber neue Mycorhizaformen, pp. 395–408.

A. Ectotrophic Mycorhizae (i. e. the fungus is entirely outside the cells of the root).

(1) The ordinary coral-like Mycorhiza of the Cupuliferae, &c.

(2) A long, branched Mycorhiza with hair-like outgrowths found on beech; the outgrowths consist of hyphae only.

(3) A somewhat similar form on *Pinus Pinaster*, but the outgrowths consist of rootlets covered with hyphae.

B. Endotrophic Mycorhizae (i. e. the hyphae enter and live in certain cells of the root).

(4) The Mycorhiza of Ericaceae.

(5) The combination of fungus and roots found in Orchids, and described by Wahrlich[1].

It is not necessary to describe in detail the new forms, but I will state what seem to be the most important points. The form (2) on the beech was found once, and it resembles at first sight an ordinary branched root—i. e. the growth in length is not interfered with, and so the 'coral-like' thickening does not occur. It appeared to be clothed with a dense pile of root-hairs. The microscopic examination showed that it was clothed with a dense thick coat of mycelium—the thickness equal to half the radius of the root—and that the apparent root-hairs were strands of hyphae radiating out from this covering. These free strands were peculiar in the hyphae, being parallel in one plane, and thus forming flat bands. Some were as long as 1½ to 2 mm. The hyphae fuse with the particles of soil as do root-hairs.

The Mycorhiza of *Pinus Pinaster* (3) is superficially somewhat like the last, but the radiating filaments which look like root-hairs are coarser, and in this case turn out to be *true lateral roots*, but so fine and closely packed that they look like root-hairs. Some were 3 mm. long and 0·1 to 0·135 mm. thick. Each of these hair-like rootlets was covered by a relatively very thick felt of mycelium. The above

[1] Bot. Zeitung, 1886.

measurement of thickness includes the mycelial envelope as well as the rootlet proper: a vascular bundle of a few elements runs down the axis. The fungus was on the outside only. No such Mycorhiza could be found on a specimen of *Pinus Pinaster* in the Botanic Garden at Berlin.

As regards the Mycorhiza on the roots of Ericaceae (4) it appears that one or two observers had already found here and there instances of association, more or less regular, between hyphae and roots.

In the Ericaceae the simpler roots may consist only of a few tracheides and sieve-tubes surrounded by relatively huge epidermal cells, each of which may occupy one-sixth of the periphery. There are no root-hairs. Each of these very large epidermal cells is filled with a dense complex of extremely fine, interwoven fungus-hyphae: these are so densely crowded that they form a sort of pseudo-parenchyma. 'In most cases these fungus elements are so fine, that one may be in doubt whether this intracellular mass is to be explained as a fungoid pseudo-parenchyma.' Frank has no doubt of this, however, since he can trace the finest hyphae from certain coarser ones which pass into the cells from the outside. The growing-point of the root of *Andromeda polifolia* is curiously reduced, and the author finds that it possesses an apical cell, triangular in surface view, from the segments of which the other tissues proceed. The dermatogen runs all round: the root-cap is reduced to two or three small loose cells; and the plerome cylinder is also extremely simple. The fungus fills the cells of the dermatogen up to the extreme apex, and the fine mesh-work alluded to above can be detected in all but the youngest cells.

On the surface of the root are loose hyphae, as a rule, and sometimes they cover the root rather thickly; even when these outer hyphae are absent, the intracellular fungus is present. In *Vaccinium Oxycoccus* the author traced the connection between the thicker hyphae outside and the finer ones in the epidermal cells, and also found hyphae running in the rather thick cell-walls. In some cases the superficial hyphae

are as delicate as those inside; they often stretch from the root to the neighbouring turf and humus remains.

Although all plants investigated had the fungus somewhere at the roots, still branches of the roots here and there were devoid of mycelium inside or out. The fungus is to be regarded as constantly present on *Andromeda polifolia*, *Vaccinium Oxycoccus*, *Ledum palustre*, *Vaccinium uliginosum*, *Empetrum nigrum*, and also the American moor-plant *Vaccinium macrocarpum*. Numerous other moor-plants showed no traces.

Further research showed the presence of the fungus on *Calluna vulgaris*, *Vaccinium Vitis idaea*, *V. myrtillus*, and even on some specimens of *Rhododendron ponticum* and *Azalea indica*. On the other hand, the mycelium was not present at the roots of *Pyrola*—a statement which corrects Kerner's short announcement (Sitzung. d. Akad. d. Wissensch. in Wien, 4 Mar. 1886: see footnote to Frank's paper, p. 401) that he had found the fungus on all Pyrolaceae, Ericineae, and Vaccineae.

The Mycorhiza of *Monotropa* is, as we have already seen, an ectotrophic form, agreeing with the typical form found on the Cupuliferae.

Frank therefore claims to have established a case of root-symbiosis in the Ericaceae, of similar biological significance to that assumed for the Mycorhiza of Cupuliferae. The epidermis-cells filled with hyphae 'constitute the most important organ of the whole root, and the sole apparatus for the absorption of nutritive materials, and abut internally directly on the conducting paths of the root.' If we suppose the cell-walls of the epidermis away, then the fungus alone would remain as the medium for conveying nutritive substances to the root.

Enough has been said to show how Frank has gradually been led to extend his original idea of a Mycorhiza, so as to include not only the type of shortened, thickened, coral-like Mycorhiza of the Cupuliferae, but also any root which has a fungus mycelium definitely associated with it, in such a way

that the root and fungus may be regarded as symbiotically related one to another. Of course this paves the way to a still wider definition of the idea Mycorhiza, and a concomitant risk of vagueness; in fact, Frank has himself had to go much further, as will be seen from what follows.

Frank's second type of endotrophic Mycorhiza is that of orchids. It has long been known that the roots and rhizomes of exotic and native orchids contain hyphae, which live in the cells of the cortex. In 1886 Wahrlich[1] carried out a masterly investigation of the subject, along the well-known thorough lines for which the Strassburg laboratory is so celebrated, and showed that the fungus in question is a *Nectria*. Reference must be made to Wahrlich's paper for details. He examined more than 500 species and all had the fungus. Aerial roots are infected as well as others.

The fungus only affects spots here and there, its hyphae coiling themselves up in certain cells into knots, which as a rule only partly fill the cell and do not destroy the protoplasm but cause the cell to enlarge.

Frank lays stress on the following points: (1) The protoplasm of the cell and the fungus live together, 'without the former being parasitically affected or its vital phenomena disturbed.'

This can only be an assumption, and the impression I gather from the study of what is known of this orchid-fungus is in favour of the view that the fungus *does* disturb or 'parasitically affect' the protoplasm of the cell, and that an outward and visible sign of some such action exists in the hypertrophy of the cells affected, and in the turning yellow of the chlorophyll-grains[2]; moreover, as Frank himself points out, the nucleus of the affected cell is larger. The conclusion that the fungus does not act as a ruthless parasite is warranted by the facts; but not so the conclusion that the hyphae do not stimulate the cells to increased metabolic activity.

[1] Bot. Zeit., 1886, pp. 481-499.

[2] Wahrlich, l. c. p. 484.

Frank's second conclusion is (2) that the root and the fungus increase together; as the root-cells divide, the fungus passes forward cell by cell. (3) The fungus is strictly connected with that part of the plant which absorbs the food-materials. 4. The orientation of the cells which contain the hyphae is such that they must necessarily act as the go-between for the absorbed substances and the conducting parts of the root. 5. Those orchids which are devoid of chlorophyll—and which therefore depend on the humus of the soil for carbonaceous matters—always have this form of Mycorhiza and highly developed.

We are therefore to regard the Mycorhiza as a humus-absorbing organ.

It is thus evident that, according to Frank's latest publications, the idea of Mycorhiza is to be extended to all such cases as that investigated by Wahrlich, and it follows in the opinion of several botanists that the root-tubercles of the Leguminosae will have to be included as another example; for, as I have lately shown [1], we have here an exquisite example of symbiosis between a fungus and the root. It is of course not to the purpose to enter here into details about this case, but I wish to point out how decidedly the facts observed are opposed to Frank's view that the fungus acts as root-hairs or absorbent organs to the bean. Of course, it may be replied that on this account it must be excluded from the category of Mycorhizae; if this is allowed, I think the same will follow as regards several of the others. The case of the fungus in the roots of *Juncus bufonius*[2] will also have to be taken into account in this connection, as well as a very remarkable example in *Podocarpus*, which I have lately observed and am at present investigating. And there are other instances also.

The point on which stress is to be laid at present is that in the bean (1) the mycelium of the fungus stimulates the

[1] 'On the Tubercular Swellings on the Root of *Vicia Faba*.' Phil. Trans., 1887, pp. 539–562.

[2] See Bot. Zeit. 1884, No. 24.

root in such a manner that local hypertrophy is brought about, attended with concentration of food-materials, and other signs of extraordinarily active metabolism; and (2) the root-hairs are by no means absent, but on the contrary are very numerous and well developed.

Consequently, those who are inclined to compare all the cases of symbiosis between roots and fungi, will at least be impelled to sharply discriminate between this form and that of the Cupuliferae and similar ones. Of course, this distinction implies much more. It is at least clear that the fungus-hyphae in the leguminous plant do not prevent the root-hairs from acting as the absorbing organs, or dissolving food substances, &c. for the plant.

The view to which my experiments and observations on the root-tubercles of the Leguminosae lead is the following: that the stimulating action of the fungus enables the roots to acquire relatively large quantities of nitrogenous materials from the soil. I purposely avoided raising the question as to whether or not the fungus of the bean-root tubercles affects directly the supplies or preparation of nitrogenous matter in the soil. We may now, however, survey shortly some of the suggestions that have been literally flung about lately as to the possibilities of the case under investigation, or of others like it.

First, however, let it be clearly stated that the questions raised do not affect the results obtained by Boussingault and Lawes, Gilbert and Pugh, as to the non-assimilation of free nitrogen by the higher plants. Plants have no power of directly employing the nitrogen absorbed by their leaves, &c.

But it has become a revived question of late as to whether the acknowledged sources of nitrogenous food of plants really suffice for the large crops taken from the soil, and whether the free nitrogen of the atmosphere is not perhaps 'fixed' in the soil and enabled to combine with other elements and so enrich the soil with nitrogen. The importance of the subject needs no insisting on, and it may simply be mentioned that the Leguminosae especially have repeatedly been cited

as carrying away more nitrogen from the soil than could be accounted for.

In illustration of this I may first give an abstract of a paper sent to me a short time ago by Professor Hellriegel, the Director of the Agricultural Experimental Station in Bernberg.

Professor Hellriegel's paper was published in November 1886, in the *Zeitschrift des Vereins f. d. Rubenzucker Industrie des Deutschen Reichs*[1], and deals with the question of the sources of nitrogen in Gramineae and Leguminosae respectively. He was aided by Dr. Wilfarth. The author sums up the well-known points that, while nitric acid, ammonia, and certain complex organic compounds such as urea, uric acid, hippuric acid, proteids, and certain humous constituents, &c. are available as sources of nitrogen for plants, cyanogen and alkaloids and certain other complex organic compounds are useless for this purpose. Moreover, as proved by Boussingault (and he might have added by Lawes and Gilbert), the free nitrogen of the air is unavailable[2].

It is also known that various natural processes lead on the one hand to the conversion of unavailable nitrogenous compounds into available forms, and *vice versa*; and, on the other hand, to displace such compounds in the atmosphere and soil. For example, electric discharges, the evaporation of water, and the activity of certain micro-organisms aid in rendering nitrogen available, and rain, dew, and certain absorptive properties of the soil supplement or aid the processes.

For a long time it has been generally known that the Leguminosae, especially, have what we may term a special aptitude for seizing large quantities of nitrogenous substances from the soil, and this property has become a classical puzzle in vegetable physiology.

Hellriegel has been engaged for some time with this pro-

[1] 'Welche Stickstoffsquellen stehen der Pflanze zu Gebote,' pp. 863–877.

[2] There is a short discussion of this subject in Dr. Vines' 'Physiology of Plants,' pp. 126–129.

blem; and the following is a short summary of his chief experimental results.

When graminaceous plants were sown and allowed to grow in a soil devoid of nitrogen, but to which all other necessary minerals were added in proper quantities, they developed normally until the third leaf appeared and the reserves were exhausted. The experiments were conducted in the open, care being taken that no rain fell on the plants, &c. Then the 'production' ceased suddenly. But the plants did not die—they lived as long as normal plants, only their vegetation was dwarfed. The stunted plant developed stunted and miserable organs (even barren ears), and struggled on through the season: the total dry weight increased very little, and this concerned the non-nitrogenous constituents only.

If nitrates are added at the moment when the above arrest of development sets in, the grasses go on growing normally again, and if sufficient is added the recovery is complete; if insufficient, a *gradual* passage to the starved condition sets in again. Hellriegel also finds that there is a direct proportion between the amount of nitrates added and the yield of grain, up to a certain point of course.

If ammonia salts or other nitrogenous compounds are used instead of the nitrates, the above proportion does not make itself evident, and the author finds that a pause ensues between the addition of these salts and their employment by the grasses—it is concluded that the above-named nitrogenous compounds have to be oxidised to nitrates before they can be used by the grasses. In other words, nitrification must be accomplished in the soil before the grass roots can employ the manure used.

Summing up the above results. The Gramineae are entirely dependent on the soil for their nitrogen: the atmosphere cannot furnish them with nitrogenous food, except in so far as rain or dew carry down nitrogenous compounds to the soil.

The most useful source of nitrogen for Gramineae is a salt of nitric acid, and nitrates supply them easily and completely. They employ the nitrates directly, and the yield of grain &c.

is directly proportional to the quantity of nitrates employed (so long as the maximum is not surpassed).

Moreover, nitric acid is no doubt the only available source of nitrogen for the Gramineae; when other nitrogenous compounds are offered, they only become available so long as they are oxidised to nitric acid compounds. Thus the development of the Gramineae is in direct relation to the quantity of nitric acid present in or manufactured in the soil.

Hellriegel then proceeds to show that experiments with leguminous plants yield totally different results.

If peas are allowed to germinate and grow in soil devoid of nitrogen, the result is astounding. In the same kind of soil deprived of nitrogen, in which grasses always pass into the starved condition above described, the peas *flourished and yielded a large increase.* Thus, from small culture-vessels, 20 cm. high and containing each four kilos of sand, the author got the following results.

In 1884, 13·947 gr. of peas (seed) yielded 28·483 gr. of dry substance above ground.

In 1885, 11·710 gr. of peas gave a yield (above ground) of 27·816 gr.

In 1885, also, 12·426 gr. peas yielded 33·147 gr. of dry substance.

And in 1886, 8·956 gr. peas gave 20·372 gr. dry substance. Moreover, the plants were normally growing, and even vigorous, and Hellriegel points out that such a yield as 33 gr. of dry substance from the same sources could not be obtained with barley even if nitrates were added.

Now comes the question, whence did the peas obtain the nitrogen necessary for this rank growth? 'There is apparently but one definite answer—from the air!' The soil was a pure quartz sand, repeatedly washed; the nutritive mixture contained no nitrogen compound; the distilled water was specially prepared, and free from ammonia or nitric acid. Even if it be supposed that traces of any nitrogen compound did fall into the vessels, the author points out that it would be out of account when we consider the large yield

in question; moreover, the grasses cultivated under the same conditions showed that the soil &c. could not have yielded the nitrogen.

Thus we must look to the atmosphere. Now the only conceivable sources of nitrogen yielded by the atmosphere are (1) the free nitrogen, (2) nitric acid, (3) salts of ammonia (carbonate and nitrate). Hence we must either assume that the Leguminosae have an extraordinary capacity for collecting and absorbing the nitrogen compounds from the atmosphere, or we must admit that the Leguminosae are in some way able to make use of the free nitrogen of the atmosphere.

Enormous difficulties stand in the way of direct proof. First, the author asks us to consider the following further observations. When peas are cultivated in a sand devoid of nitrogen as above, two remarkably sharp periods of development are to be noticed.

Up to the period when the reserve-materials are exhausted, the seedlings grow normally, luxuriantly, and with normal colour. But directly the reserves are exhausted, a somewhat sudden change occurs—growth stops, the leaves turn pale, and the plant evidently begins to starve.

Sooner or later, however, the pale or yellow leaves again turn green, and a *second period of growth begins,* and the plants go on growing normally to the end.

The sharply marked starvation is not reconcilable with the view that the peas take their nitrogen directly from the above compounds in the air. When the reserves begin to be exhausted the plants have each about six leaflets; how are we to explain that these six leaflets suddenly and so completely fail, and that just at this particular period the plant becomes unable to use the nitrogen supplied? and further, to explain why and how, after a pause, the plant begins to acquire nitrogen?

We are then asked to note the following observations. When the above cultivation experiment is repeated on a large scale, it is noticed that the development of the individual plants—all under the same conditions—is very unequal. Some, usually few, grow very vigorously as said;

others close beside these do worse; and yet others may never pass through the starvation-period. It occurs not rarely (and this is expressly insisted upon) that of two peas growing side by side in the same vessel, the one starves and the other succeeds in the highest degree.

Now, since it is impossible to assume, in earnest, that peas have the power of growing without nitrogen in the soil, and at one time to succeed and at another to fail, the only explanation is that the above extraordinary behaviour of the control-plants in well-arranged experiments, is that there is, in addition to the known and carefully regulated factors, *some unknown* co-operating factor, which depends on accidentals and which exists outside the culture-vessels.

Hellriegel then proceeds to describe the following experiment. Four vessels were filled with soil devoid of nitrogen, and peas put in and allowed to germinate; the vessels were then placed under four glass bell-jars, enclosed, and joined by tubes, and the whole so arranged that a constant stream of air was drawn through from No. 1 to No. 4. Absorption-vessels were placed between each pair of bell-jars, and matters so arranged that the air passed into No. 1 unaltered, but, before entering Nos. 2, 3, and 4, was deprived of ammonia and nitric acid. The pea-plants were each about 15 cm. high, and had passed successfully through the above-named starvation-phase, and entered into the second lease of existence. This continued under the bell-jars, and, in short, all the plants flourished, and attained an average height of 120 cm., and had entered upon the flowering and fruiting stage when the experiment was stopped. The results were—

No. 1 = Ordinary atmospheric air, yielded 13·6 gr. of dry substance in the straw, and 3·4 in the roots, = 17 in all.

No. 2 = Purified air, yielded 14·6 in straw, and 3·5 in roots, = 18·1 in all.

No. 3 = Purified air, yielded 19·1 in straw, and 3·9 in roots, = 23 in all.

And the author states that the observations lend no probability to the idea that the small traces of combined nitrogen

in the air can supply the plants with what they obtain, 'and probably the only assumption which remains is that the Papilionaceae have the power of making the free nitrogen of the air available for their life-purposes.'

Now it has been certainly shown by Boussingault that even the Papilionaceae are unable directly to assimilate the elementary nitrogen; but this does not exclude the possibility that something of the kind may occur indirectly, and we have now to examine a few observations which may point to something of the kind.

Berthelot has shown that free nitrogen may be absorbed by the soil and converted into compounds, probably by means of schizomycetes or micro-organisms of some kind. The roots of Papilionaceae are provided with tubercular swellings full of 'bacteria'.[1]

It has been stated above that in the researches some plants did well and others worse: now, Hellriegel finds that those plants which are still in the starvation-phase have either no tubercles or very few and insignificant ones, whereas the plants which are flourishing have many well-developed specimens on the roots. 'The more plants we investigated, the more we were convinced that the development of the root-tubercles stands in the closest, strictest relation to the growth and assimilation of the whole plant.'

Now, notice the following experiments. On May 25 were taken forty vessels filled with soil devoid of nitrogen, and two pea-seeds placed in each. Then ten of these vessels were watered with soil-washings—the authors say, 'Resting on the fact that in every normal culture-soil micro-organisms exist in abundance, we took some of the fertile soil of our culture-field, stirred it up with five times the quantity of distilled water, and after a short settling gave 25 cc. of this quasi-solution to each vessel.'

Bearing in mind that the experiment began on May 25,

[1] Here the author is following older views as to the nature of the contents of the tubercles: they are not bacteria, but yeast-like gemmules budded off from the mycelium of a true fungus. (See paper in Phil. Trans. 1887, pp. 539–562.)

the early phases were passed through, and in the second week of June the aspect of the plants was changing, and they became pale as the reserve-materials were exhausted.

So far, there was no difference to be observed between the forty cultures.

On June 13, however, a difference began to set in, and by June 18 it was decided—'In the ten vessels supplied with bacteria[1], all the plants had regained their fresh green colour, and commenced to grow vigorously.'

Of the thirty vessels in which the appearance of micro-organisms was left to chance, only two at this time presented a similar appearance, the remainder starving and in part yellow.

By the 30th of June, the plants supplied with bacteria were developing the tenth leaf, and were luxuriant; only one of the twenty individuals was behindhand, and the deep green colour showed this was not from want of nitrogen—later examination showed that its tap-root was injured.

Of the sixty plants not supplied with bacteria, about ten were nearly as flourishing as the above, and five were nearly dead: among the remaining forty-five were all stages between these extremes.

At this time the plants from two of the vessels infected with bacteria and those from five of those not so infected were taken up and examined, and showed the above-described relation between the growth of the sub-aërial parts and the development of the root-tubercles.

Of twenty-two plants to which no bacteria were added, only five yielded more than 15 gr. dry substance, as follows—

No. 2 = 15·053
„ 26 = 15·950
„ 29 = 17·142 } gr.
„ 18 = 17·305
„ 1 = 20·372

The yield of the remaining seventeen plants was between 1·640 gr. to 13·190 gr.

[1] Here again it is of course an assumption that 'bacteria' were the agents.

On the other hand, the yield of the plants in four vessels supplied with the 'bacteria' (and these were not the best) was in every case more than 15 gr. dry substance:—

No. 31 = 15·789
„ 32 = 18·768
„ 36 = 19·743
„ 40 = 16·200
} gr.

Hellriegel then points out that the uniformly and decided large yield in the latter cases must have been due to the co-operation of the micro-organisms, for since in each case the 25 cm. of fluid added contained less than 1 mg. of nitrogen, we cannot suppose it due to that.

Two cultivations were made in soil without nitrogen, to which nutritive materials and 25 c.cm. of the above soil-washings were added, and then the whole sterilised by heating, then the seeds sown, and then covered with a layer of sterilised wadding. All went well until the development of the sixth leaflet, and the setting in of the starvation-phase. The plants never recovered, however; all died. 'No trace of tubercles was to be found on their roots.'

Passing over other experiments, which lead to the same general result, I may sum up Professor Hellriegel's results in his own words:—

'The Papilionaceae, in contrast to the Gramineae, are not dependent on the soil for their nitrogenous nutrition; the sources of nitrogen afforded by the atmosphere have for these plants the highest importance, and are alone sufficient to bring them to normal and even luxuriant development.'

. . . .

'It is seen that not one of these observations supports the idea that the sources of nutriment of plants are to be sought in the small quantities of combined nitrogen which are found in the atmosphere, and thus probably the only remaining assumption is that the Papilionaceae have the power of making use of the free nitrogen of the air.'

. . . .

'To the nutrition of the Papilionaceae, and especially to

the assimilation of nitrogen by them, the so-called tubercles and the micro-organisms which dwell in them stand in the closest active connexion." . . . .

The following remarks may be made respecting this paper. It is above all unfortunate that the authors do not give us more details as to the analysis of their crops: in the absence of exact numbers, their conclusions as to the increment of nitrogen can scarcely be criticised. It must also be pointed out that the tubercles referred to do not contain bacteria, but that the "bacteroid" bodies are minute yeast-like gemmules budded off from the hyphae of a true fungus which enters the root-hairs, crosses the cortex, and branches out in the tubercles.

Before making any further observations, I may quote the following:

In August 1888 a paper was published by Frank, on the sources of nitrogen of plants, in which the author points out that Schultz-Lupitz and others have shown that Leguminosae will grow for years without any marked decrease in produce unless on a soil which is barren, provided all other needful salts are supplied except the nitrogenous ones; and that crops of Leguminosae preceding Gramineae on a poor piece of land enrich the latter in nitrogen. He then points out that three kilos per hectare is the most that could be supplied annually from the combined nitrogen washed down by rain from the air, whereas a normal yield corresponds to about fifty-one kilos of nitrogen per hectare.

In experiments with finely sifted soil consisting of sand and humus the following results were obtained. A quantity of the soil was analysed: a second lot was put in vessels, and some leguminous plants sown in them; a third lot was allowed to stand in pots alone.

All were exposed to the air, and watered with distilled water, and protected against insects. In the control-pots, all weeds were carefully removed as they sprang up.

[illegible] Stickstoff-nahrung der Pflanzen. Ber. d. deutsch. bot. [illegible]

Before giving his own results Frank summarises those obtained by some other observers.

Dietzell[1] found with peas and clover that there was a loss in nitrogen during the progress of experiments similar in principle to these.

Berthelot[2] found that the soil itself can fix free nitrogen in combination, and that the process may depend on the activity of micro-organisms. The increase was not in the form of ammonia or nitrates, but as organic compounds. Sterilisation destroyed this power on the part of the soil.

Joulie[3] found similar results. He cultivated plants in pots, and the nitrogen increased.

Frank's results are shortly as follows. In the soil with no plants there was a gradual loss of nitrogen; in those in which the plants grew there was an increase in many cases. Frank concludes that 'the increment of nitrogen here observed can only be looked upon as a fixation of uncombined atmospheric nitrogen, unless we assume that this large quantity of ammonia has been seized from the air by the plant.'

Frank further concludes that two processes occur side by side in the soil—one which results in the freeing of nitrogen from its combinations in the soil, and another which consists in the fixation of nitrogen from the air—'the latter is favoured by the presence of living plants.'

Some experiments made by Dr. Vines in 1887, and communicated to the British Association at Manchester, also bear on this subject. Dr. Vines cultivated beans in a medium devoid of nitrogen, and found that they went on growing much as if nitrogenous food-materials were present at the roots.

The following paper is quoted simply to give an example of publications bearing on another aspect of the same question.

In 1873 M. Dehérain published a paper in the *Annales des*

[1] Sitzung der Section fur landw. Versuchsw. d. Naturf. zu Magdeburg, 1884.
[2] Compt. Rendus, 1885, p. 775.
[3] Ibid. p. 1010.

Sciences Naturelles[1] on the subject of the relations of the atmospheric nitrogen to that of plants. After pointing out that a forest, regularly exploited, loses annually when the trees are cut certain quantities of nitrogen, and that large pastures &c. do the same, and this goes on year after year without any apparent restitution further than what is afforded by the manure of animals, decay of organisms, &c., he then proceeds to show that the opinion gains ground that the soil seems to lose more combined nitrogen than it receives, and the only explanation of the anomaly is that the atmosphere's free nitrogen intervenes.

The author then considers the question of the losses and gains in nitrogen of cultivated soils.

Regarding, first, the losses: they are as follows:—

(1) Losses of combined nitrogen, due to—

(α) Excess of nitrogen carried off in crops.

(β) Washed away by rain from soil.

(γ) Lost in drainage through subsoil.

(δ) Loss of ammonia diffused into the air.

It is only necessary to note that various observers have shown that in a rotation of crops more nitrogen is carried off in the total crops than was contained in the manure, supposing the latter completely utilised. The examination of streams and of drainage-waters gives some idea of the loss by superficial and subterranean water: quoting one case only, the Rhine and Seine were calculated to carry off about 200,000 kilograms of nitrates annually.

With respect to ammonia diffusing into the air; not all the ammonia of the soil is oxydised to nitrates, but some forms volatile compounds—e.g. the carbonate.

(2) Dehérain then proceeds to examine the loss of free nitrogen.

It appears that whenever decomposition of organic matter occurs, there is, in addition to ammonia, free nitrogen also evolved: the chief condition necessary is active oxidation.

[1] Vol. xviii. Ser. 5, 'Recherches sur l'intervention de l'azote atmosphérique dans la vegetation,' p. 147.

The second part of the paper is devoted to the consideration of the gains in nitrogen of the soil. First, we have the gain in combined nitrogen:—

Ammonia and nitric acid found in the atmosphere during electric discharges, and carried down by rain, snow, &c. This can be measured and shown to be too small to account for the nitrogen acquired by plants in addition to that in the soil, &c.: this is admitted fully since Boussingault, and was clearly evident in the experiments of Lawes, Gilbert and Pugh [1].

We then come to the chief points in Dehérain's paper:—the gains due to the fixation of free nitrogen.

It is unnecessary to discuss the question of the 'assimilation' of nitrogen by the plant direct: it is allowed on all hands that the experiments of Boussingault, and of Lawes and Gilbert, settled that point for ever—no free nitrogen is assimilated by the leaves.

Dehérain experimented with various combustible—i.e. easily-oxidisable bodies, such as carbo-hydrates, old wood, &c., in contact with certain bases. Such mixtures exposed to the air were found to absorb and 'fix' not only oxygen but also certain quantities of free nitrogen.

The explanation first suggested was that some of the oxygen and nitrogen of the air unite to form nitric acid at the moment of combustion, just as they do when hydrogen is detonated with air; but it turned out that this was not the case, and the compound formed was some other combination of nitrogen—possibly a lower oxide of nitrogen, possibly cyanogen, or ammonia.

Dehérain then made experiments to determine the fixation of atmospheric nitrogen by vegetable substances. He agrees with Lawes and Gilbert in rejecting the view that ammonia is formed in damp soil simply by union of hydrogen evolved by putrefaction and the nitrogen in the confined spaces afforded by soil.

[1] Contained in their well-known paper in Phil. Trans. 1860.

The results of experiments with saw-dust, humus, roots, &c. led to the inference that free nitrogen is fixed, and that if oxygen is absent the hydrogen disengaged—being unable to form water—unites with the nitrogen to form some compound.

This led to experiments under other conditions, and nitrogen was passed over warmed mixtures of glucose and soda, and the results confirmed the authors' expectations, but are chiefly of interest as leading to other suggestions.

Experiments based on these led to the conclusion that if nitrogen is passed, in the cold, over saw-dust or glucose, alone or mixed with alkalis, some of the nitrogen is retained, 'fixed' in combination. It is thus demonstrated that, 1st, 'the nitrogen of the atmosphere may be fixed by vegetable substances, even in the cold and under conditions analogous to those which are met with in cultivated soils; 2nd, this fixation is singularly promoted by the absence of oxygen.'

Thus when organic matter decomposes in an atmosphere deprived of oxygen, or nearly so, giving rise to carbonic acid and to hydrogen, the nitrogen of the atmosphere is absorbed and unites with the hydrogen to form ammonia.

It appears that Thenard and others have shown that in the soil there are, as it were, two atmospheres—one, an oxydising atmosphere in the upper layers, the other, a reducing atmosphere lower down. Dehérain points out that 'the energy of slow combustion is much greater than is usually supposed: germinating seeds in a closed space absorb the oxygen, even to the last trace, in a few days; aquatic plants kept in water in the dark take from it all the oxygen it contained. If the composition of the air confined in a heap of manure is determined, there is found only nitrogen and carbonic acid mixed with a slight proportion of combustible gas, oxygen is absolutely wanting. This is an experiment which we have repeated at Grignon for several years without variation.'

Thus there is in the soil, at a certain depth, an atmosphere devoid of oxygen—the decomposition of organic substances may give rise to hydrogen—the latter may meet with nitrogen and form ammonia.

I now pass to a summary of several other papers recently published, and bearing on the general question: they must, of course, stand on their own merits. In 1885 Berthelot[1] showed that the amount of combined nitrogen in pots of soil, exposed for some months to the atmosphere, continually increased; this was proved to be due to the absorption and 'fixation' of free nitrogen, and much in excess of any nitrogen compounds that could be supplied in rain, &c. Berthelot showed also that this action does not occur if the soil is sterilised by heat, and concludes thence that the action is due to the intervention of living organisms. The process, moreover, comes to a standstill in the winter, and is at its best when vegetation is most active.

The author concluded that in six months more than 26–32 kilos of nitrogen per hectare would be absorbed in his experiments.

In 1886, M. Berthelot[2] published further results, showing that nitrogen is continually absorbed from the air, even when no plants are being grown in the soil. The amount absorbed is in all cases very much greater than the quantity of nitrogen existing as ammonia or nitrogen oxides in the air or rain. Much of the absorbed nitrogen is converted into nitrates.

In the Comptes Rend., T. 104, p. 625, Berthelot again publishes results on this subject, especially referring to soil in which plants are being grown, and finds that less nitrogen is fixed than was the case with fallow soils. A further paper appears by the same chemist in the same volume, showing that, independently of the other processes, ammonia is continually being evolved from vegetable soils. This double action—fixation of nitrogen on the one hand, and the escape of ammonia on the other—has been noted by other observers also.

In the 'Proceedings of the Royal Society' for 1887[3], Messrs.

[1] Compt. Rend., T. 101, p. 775. [2] Ibid. T. 104, p. 205.

[3] Proc. Roy. Soc., p. 108, 'On the present position of the Question of the Sources of Nitrogen of Vegetation, with some new results, and preliminary notice of new lines of Investigation.'

Lawes and Gilbert give a resumé of the question of the sources of nitrogen in plants, and especially of their further results. In their earlier paper they concluded that, except the small annual increment of combined nitrogen washed down by rain, the source of nitrogen was substantially the stores in the soil. The compared growth of gramineous crops and of leguminous crops under parallel conditions resulted in the conclusion that more nitric acid accumulated in soils under Leguminosae, indicating increased nitrification.

Attempts to explain the increase of nitrogen under Leguminosae as due to the subsoil, or to the action of acids in the roots, &c., failed.

References are then made to the experiments of Berthelot and André, and of Loges, showing that the insoluble nitrogenous substances in soils are of the nature of amides.

Experiments are then adduced showing that green plants can take up soluble complex nitrogenous organic bodies in water-cultures, and possibly they can take up amides in the soil.

Frank's researches on Mycorhiza are then referred to: of course only the earlier paper is quoted. Then comes in the question of the participation of free atmospheric nitrogen, and the authors reserve their opinion, pointing out, however, that the soil contains enormous quantities of combined nitrogen, and that there is 'obviously still a wide field for enquiry as to whether or not, or in what way, the very large store of already existing combined nitrogen may become available to growing vegetation.'

In the above citations it is not by any means to be implied that a complete survey of the literature has been given or attempted; several papers have been passed over as either generally known, or too technical for the present purpose, and of course there is still much discussion on many points—e.g. as to the *modus operandi* of nitrifying organisms[1], as

[1] See Schlœsing and Muntz in Comptes Rendus, 1879; Warington, Chemical News Journal, 1879 onwards; and Berthelot, Comptes Rend. 1876 onwards.

to the view that nitrogen is fixed by organic substances in the soil during slow electric changes, and so on.

The chief points to be summarised seem to be these. There is a general tendency to the view that the Leguminosae at least take more nitrogen from the soil than can be accounted for if the only sources are (1) the combined nitrogen of the atmosphere washed down into the soil, and (2) the combined nitrogen of the soil found by analysis of samples. It is therefore surmised that the free nitrogen of the atmosphere is 'fixed' under such conditions that it can combine with other elements, and so supplies the deficiencies.

In favour of this are quoted the experiments of Berthelot, Frank, Hellriegel, and others. As a point against the *necessity* of this—not as against the facts of such fixation—Messrs. Lawes and Gilbert especially remind us that sub-soils may and do contain large quantities of combined nitrogen, and it is still questionable how far these can be carried up into the soil, or reached by the roots of deep-rooted Leguminosae.

It should be noted that the water of the sub-soil (containing dissolved substances) may rise for long periods in dry summers, when the plants above are transpiring, by capillarity; hence the adduced increase of nitrates in the upper parts of the soil during active vegetation is not in itself a proof of absorption from the air. Of course this does not apply to pot-plant experiments.

Then comes the consensus as to nitrification by means of organisms in the soil. But it must not be overlooked that the usual case consists in the oxidation of nitrogenous compounds already present in the soil.

The startling point in Hellriegel's experiments—more cautiously entertained by Frank and Vines—is that organisms co-operate in the fixation of *free nitrogen* under such conditions that it then enters into combination. That we are here face to face with a difficulty must be clear to every one.

In conclusion, it seems that we cannot, as yet, clear up

the question as to whether the fungus of the Leguminosae aids in the fixation of free nitrogen, and we cannot regard it as proved that the fungi of Frank's Mycorhiza take any part in providing the plant with nitrogenous elements, however probable it may appear. Moreover, I may suggest that the cases are not quite similar: in Frank's observations the fungus may merely hurry the decomposition of organic remains. With respect to the alleged absorbent function—or root-hair function—of Frank's fungi, it is only necessary to point out that it is difficult to imagine how a fungus hypha with its low and peculiar organisation can assume the remarkable and by no means simple functions of root-hairs: the anatomical facts are in Frank's favour, so far as they go, in reference to the Cupuliferae, but of course it is always hazardous to attempt to explain physiological problems simply on anatomical evidence.

With respect to *Vicia Faba*, there are no reasons for supposing that the fungus replaces the root-hairs functionally in any way; the experiments of Hellriegel, Frank and Vines, point to the possibility of its aiding in rendering nitrogen available, in some way as yet unexplained; and my own observations point to the probability that it stimulates the roots to absorb and use whatever nitrogenous materials are present with extraordinary avidity. One consequence of this is, no doubt, increased respiration,—i. e. a more rapid rate of absorption of the oxygen in the soil; but whether we can go further than this needs investigation, though it may have a bearing upon Dehérain's suggestion.

As regards the Leguminosae, therefore, we are still face to face with two distinct problems, quite independent of the old one as to the parasitic nature of the tubercles, which has been solved by my discovery of the causal fungus entering the root-hairs and stimulating the root-cortex locally. These two problems are: (1) Does the fungus in question directly co-operate in the absorption of food-materials from the soil, nitrogenous or otherwise? and (2) Does the fungus take any part in the preparation of nitrogenous substances, or the

absorption and fixation of free nitrogen, so as to render them available to the plant?

If Hellriegel's results are confirmed, the last question is answered generally, the further enquiry narrowing itself into, How can the fungus act in the fixation &c. of free nitrogen? But the previous question will still remain to be answered, the evidence at present being distinctly against the view that the fungus aids directly in absorbing food-materials, and in favour of the supposition that it stimu'ates the plant to greater metabolic activity. It is only fair to add that the possibility that the combined fungus and stimulated cells—i.e. the root-tubercles—may act, as a whole, as a compound organism possessing the power of making use of the nitrogen, is not to be set aside as absurd so long as the question of a nitrifying organism can be entertained at all.

NOTES.

ON ACALYPHA INDICA, Linn.—At the foot of the account of the large (220 species) Euphorbiaceous genus *Acalypha*, Mr. Bentham (in Benth. et Hook. f. Gen. Pl. v. 3, p. 311) states;—'In *A. indica*, Linn., speciebusque nonnullis aliis tam Americanis quam Gerontogeis, spica androgyna superne mascula saepe terminatur

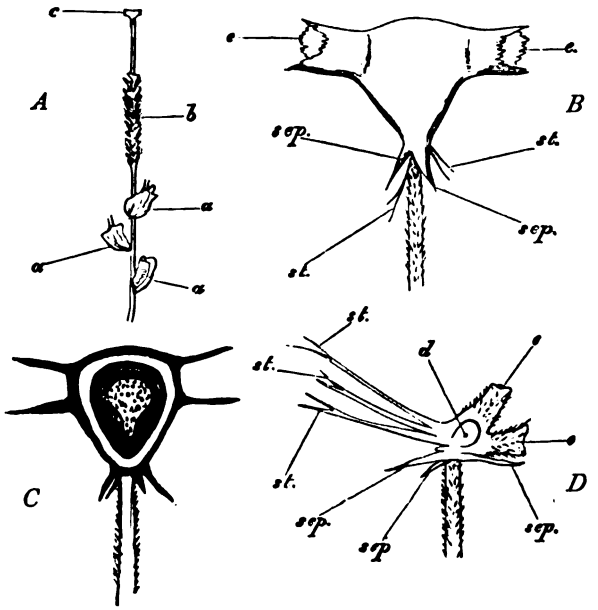

FIG. 6.

flore parvo longe pedunculato heteromorpho foemineo vel subhermaphrodito varie obliquo vel recurvo, quoad perianthium et ovarium imperfecto saepius tamen fertili capsulâ monospermâ.'

Mueller, Argov. in DC. Prodr. v. 15, pars. 2, p. 869, says of *A. indica*:—

'In speciminibus variis saepe occurrunt spicae apice monstrose terminatae, apice quasi abeuntes in setam filiformem, gracillimam, apice

calyculum 3-partitum et corpusculum obovoideum truncatum fere bicephalum cavum utroque latere apertum et fimbriato-incisum gerentem.'

This termination of the spike is so common and so characteristic of the species in India that it is prominently shown in the figures, Rheede, Hort. Mal. v. 10, t. 81, and in Wight, Ic. t. 877. Wight gives an enlarged picture of it—his Fig. 2—of which his explanation is 'portion of a spike showing both male and female flowers with its terminal cross.'

Bentham's explanation is taken from the drawings and notes in my herbarium dated 1868 and 1871, and which here follow.

Fig. 6, A, is the summit of a flower-spike, natural size. *a*, *a* are the bracts, each of which conceals a normal female flower having three cells to the ovary, and ripening often three carunculate seeds with superior radicles; though in these 'cross-bearing' spikes the lower female flowers are frequently barren. *b* is the dense narrow cylindric spike of small male flowers. *c* is the terminal cross, usually subsymmetric in ripe fruit.

Fig. 6, B, represents the terminal cross enlarged, and Fig. 6, C, represents a vertical section of Fig. 6, B. It contains a single perfect seed with regular embryo, and the seed is nearly normal except that the caruncle is obsolete, and that the radicle is inferior as regards the axis of growth. *sep.*, sepal; *st.*, withered stigma; *e*, probably barren loculus of ovary.

Fig. 6, D, is a facsimile of my sketch in 1871 of the terminal cross when young. The sepals, *sep.*, are somewhat distorted: but the flower is as it were pressed down horizontally; the three styles, *st.*, with bifid tips are normal, but stick out sideways; one loculus of the ovary, *d*, contains the ovule, in its normal position as regards the loculus; the two processes *e*, *e*, I marked doubtfully as the two barren loculi. As this monstrous ovary ripens the turning is carried further from the normal till it takes almost a reversed position.

Thinking these notes sufficiently curious for publication, I put them (with the material on which they were founded) aside apart from my other Euphorbiaceae, and have just lighted on them in distributing some old collections. I regret that thus, while I placed them before Mr. Bentham when he was engaged on *Acalypha*, they did not come before the notice of Sir J. D. Hooker when he was working up the Euphorbiaceae for the Flora of British India. The above explanation is, I hope, right so far as it goes; but should be regarded, as Professor Oliver observes, as calling attention to a point deserving (and easily admitting) further investigation.

C. B. CLARKE, Kew.

CALCAREOUS DEPOSIT IN HIERONYMA ALCHORNEOIDES, Allem. The following note may be of interest to readers of the 'Annals of Botany':—

ROYAL BOTANIC GARDENS, TRINIDAD,
Jan. 19, 1888.

DEAR SIR,

I send you by this mail a piece of wood from the trunk of a Euphorbiaceous tree (*Hieronyma alchorneoides*, Allem.). In it and on the outside is a curious deposit, called by the native sawyers 'stone.' This material is a great nuisance to them, as it blunts their saws. The wood is a very useful one, and is known locally as Tapanâ—Tapanare in Spanish. My attention was called to this deposit by Mr. C. W. Meaden, Superintendent Convict Depôt, Chaguanas, who does considerable timber cutting. Considering it to be worth examination I asked the Government to allow an analysis to be made by Mr. McCarthy, the results of which are given below.

Calcium as carbonate (Chalk)	85·81
Loss on ignition, woody fibre and some carbonic acid gas	5·06
Insoluble in acids	·76
Alumina, including phosphates and iron . .	8·37
Total	100·00

Mr. McCarthy further remarks, 'In my opinion the land on which the "Tapanâ" tree in question was grown contained a fair proportion of lime. This lime was dissolved by the rain water containing carbonic acid gas, and the solution was subsequently assimilated. During the circulation of the sap and at a certain height an outlet was reached[1], when the gas essential to the dissolving the lime parted company with the solution, and as a result the lime was deposited as it is on the inside of a boiler or tea-kettle.'

The deposit occurs in cracks or fissures which may be caused by the action of the air or may be caused by the concussion when the tree is felled to the ground.

The fact, however, would appear to be new[2] that wood should make

[1] Fissures caused by fall probably.—J. H. H.

[2] Deposits of phosphate of lime in teak are well known Quart. Journ. Chem. Society, Vol. xv. p. 91).—W. T. T. D.

a deposit on the surface and in the cells of the tree which contains 85·81, or nearly 86 per cent. of calcium carbonate.

(Signed) J. H. HART,
Superintendent.

D. Morris, Esq., M.A.

As an addendum to the report upon the exudation upon 'Tapana' wood I should mention that the soil near which the tree was grown contained on analysis the following :—

Moisture at 212 F.	1·24
Water of combination and organic matter	3·86
Oxides of iron and alumina with phosphates	7·73
Lime	·15
Sulphuric Acid	Traces
Magnesia	·18
Potash	·10
Soda	Traces
Silica, sand, &c.	86·74
Total	100·00

W. T. THISELTON DYER, Kew.

ON THE POWER OF CONTRACTILITY EXHIBITED BY THE PROTOPLASM OF CERTAIN PLANT CELLS.—In a communication to the Royal Society (see Roy. Soc. Proc., No. 240, 1886), I gave some account of the principal changes which take place in the gland-cells and stalk-cells of *Drosera dichotoma* during secretion, and later I gave a preliminary account (see Roy. Soc. Proc., No. 260, 1887) of certain experiments and observations which were undertaken in order to attempt to ascertain by what mechanism the bending of the tentacles is made possible in *Drosera*, and what changes occur in the tentacle-cells. I hope shortly to publish a full account of my observations in the 'Annals of Botany,' but in the meantime the following note, which is almost a reprint from the Roy. Soc. Proc., will indicate the line of my work.

During actual movement no obvious histological changes can be detected in the cells of the bending portion, but when the tentacle has become well inflected, it becomes apparent that the cells of the

convex side become more, and those of the concave less turgid than before. Some time after stimulation, and when the period of aggregation has set in, it can be observed that the cells of the convex side are less aggregated than those of the concave. Having ascertained that of the dye solutions, eosin, and of salts, the salts of ammonia, are readily sucked up into the tissue, it was further noticed that in stimulated tentacles the cells of the convex side readily allow the solutions to penetrate, while those of the concave are only penetrated with great difficulty. Thus in the case of a stimulated tentacle treated with eosin, the convex cells are stained long before the concave, and with ammonic carbonate the tannin of the convex cells may be precipitated while the concave cells remain normal, or the convex cells may even be killed while the concave cells remain alive. Thus after stimulation certain changes have occurred in the concave cells of the bending portion, and one result of this change is an increased impenetrability of the primordial utricle. In my earlier paper I have shown that the tentacle cells of *Drosera* are very sensitive to contact, for if the gland-cells be slightly crushed, all movement of the stalk-cells ceases for a time, and the spindle-shaped rhabdoid contracts and tends to become spherical. Bearing in mind also the very pronounced inflection which is occasioned by the stimulus of contact or food, by electrical stimulus or, as Darwin has shown, by the stimulus of temperature, one is led to ask whether these phenomena are not associated with true contractility, and whether the increased impenetrability of the protoplasm of the concave cells is not occasioned by a definite contraction of the primordial utricle and a consequent decrease in the size of the molecular pores.

Experiments were then made upon the pulvinus of *Mimosa pudica*. Small pieces of stem (bearing leaves) were cut under a watery solution of eosin, and the pulvini were maintained in a state of stimulation. When the eosin had sufficiently penetrated, transverse and longitudinal sections of the pulvinus were made and examined. It was then seen that the dye had readily penetrated into and stained the protoplasm of the outer cells of the convex side of the pulvinus, while on the concave side no staining whatever, of that tract of cells situated towards the more external portion, which especially play an active part in movement, had taken place. The more indifferent cells immediately surrounding the vascular bundle also show some contrast in coloration, for in the upper half this tissue remains unstained,

while in the lower half some staining occurs. Thus, by the process of staining, the seat of the especially irritable tissue was clearly brought into view. I now commenced electrical experiments with the pulvini. Two small pins (which were found not to injure the tissue to any appreciable extent) were inserted into the irritable tissue—one at each end, and fine wires from these pins communicated with the various electrical apparatus as required. When suitably stimulated with either a constant current, an induction shock, or a tetanising shock, the leaf fell immediately contact was made. With the single induction shock the breaking shock was found to be a stronger stimulus than the making. A small piece of stem with the pulvinus attached—the lamina and a portion of the petiole of the leaf having been previously removed—was attached to a lever which wrote upon a revolving drum. On throwing in the electrical stimulus the pulvinus contracted and a curve was obtained. The pulvinus was then turned upside down, and, after recovery, was again stimulated and a second curve obtained. In both instances the pulvinus raised a weight greater than that of the leaf and leaf stalk. These experiments for the most part only confirmed those of Cohn and Kabsch, except that they were carried out in further detail; but one new and important observation was made, viz. that under the influence of a feeble tetanising current the period of recovery of the pulvinus could be materially shortened, and the leaf could be induced to assume the position before stimulation in less time than it would have taken under ordinary circumstances. The wonderful delicacy with which the irritable cells of the pulvinus at once reply to stimulation, the fact that in their reaction to the stimulus of electricity they obey the same laws as animal muscle, and, like certain muscles, may also be relaxed by a feeble tetanising current, go far to suggest that in dealing with the movements of the pulvinus of *Mimosa* we have essentially to do with the phenomenon of contractility.

Although the foregoing results may be said to favour the idea that in irritable organs movements are brought about by a definite contraction of the protoplasm of the cells of the irritable side, yet I felt that the matter could only be set at rest by still further strengthening the evidence, and if it were possible, by the actual observation of a cell contracting under the influence of electrical or other stimulation. I therefore turned my attention to the simple filamentous Algae, and among them to an organism which I believed would be peculiarly

sensitive to stimulation, viz. *Mesocarpus pleurocarpus*. The filaments consisting of rows of cells were first experimented upon electrically. A single induction shock of moderate strength was found to cause a splitting apart of the previously united transverse walls of the contiguous cells along the middle lamellae. In each cell, the two end-walls now project inwards towards the centre of the cell in a concave manner, so that between each pair of cells of the filament there arise a series of double convex lenticular spaces. The rupture does not extend to the free surface.

With a stronger shock so much contraction is produced that the cells actually fly apart and a complete rupture is effected. The end-walls of each cell are now observed to be slightly convex instead of concave. This is a result of the contraction of the freed edges of the external walls, which in consequence of the rupture no longer maintain their cylindrical form. Each cell now resembles a cylinder with its two ends somewhat convex, and its sides very slightly contracted in the immediate neighbourhood of their lines of union with the ends. As in *Mimosa*, the breaking is a stronger stimulus than the making shock. Similar contraction is obtained with the tetanising shock and with the constant current.

Sudden illumination, sudden rise of temperature (45–50° C.), and the stimulus of certain poisons, bring about the contraction and breaking apart in the most marked manner. Of the poisons, camphor, quinine, strychnine, physostigmine, and strong alcohol were found to be exceedingly powerful, with very dilute alcohol no obvious change occurred. The strongest plasmolysing reagents did not bring about the rupture of the cells, but only the partial separation of the end-wall, and if the cells are killed by boiling water, by iodine, or by very dilute chromic acid (0·25 per cent.), similar results follow. With 1 per cent. osmic acid or 1 per cent. chromic acid the cells may be killed and fixed with little or no contraction.

The results with plasmolysis entirely agree with those previously obtained in the case of *Drosera* (loc. cit.): the protoplasm seeming to be partially paralysed, and the whole of its energy apparently expended in endeavouring to protect itself from the abnormally rapid withdrawal of water. The passive shrinking produced by strong dehydrating reagents is essentially different from the active contraction arising from normal stimulation, and one may well inquire whether the effects produced by plasmolysis at all tally with those vital

processes which actually take place under ordinary circumstances in plant-cells.

The results obtained with *Mesocarpus* demonstrate that we have here a plant-cell which reacts in a most powerful manner to the stimulus of temperature, of light, of electricity, and of poisons, and that this reaction, which may be watched under the microscope, is attended by a diminution in size. In my opinion such a series of reactions can only point to one property of the protoplasm, viz. that of contractility, and taking into consideration the whole of the observations, there appears to be no doubt that the protoplasm of plant-cells, like that of animal cells, is capable of active contraction. I believe that in all irritable organs the movements are brought about in consequence of a definite contraction of the protoplasm of the irritable cells, and that during such contraction some of the cell-sap escapes to the exterior. At the same time the elastic cell-wall contracts *pari passu* with the protoplasm. I have already drawn attention to the intimate connection between the protoplasm and the wall (Phil. Trans. 1883, Part 3), and have shown that even after pronounced plasmolysis, the ectoplasm of the primordial utricle is always connected to the cell membrane by very numerous and delicate strands of protoplasm. The protoplasm may be withdrawn from the wall by a very strong electric shock, but the normal effect of a moderate stimulus is to cause the protoplasm to contract, and in certain cases pull upon its wall, while in very turgid cells, where the cell-wall is in a state of great tension, the wall for the most part simply contracts upon the protoplasm. The escape of liquid from the interior of the cell is regarded as being due to filtration under pressure. I am unable to uphold Pfeffer's theory that the sudden abolition of turgidity is dependent upon the destruction of a certain quantity of an osmotically active substance. In my opinion there is in every cell a sufficient quantity of osmotically active substance to ensure turgidity, but the increase or decrease of turgidity essentially depends on the contraction or relaxation of the primordial utricle. My experiments all tend to show that it is the ectoplasm which mainly determines the state of turgidity of the cells. Thus in the tentacle cells of *Drosera* the endoplasm may partially be withdrawn from the ectoplasm by the lengthy action of strong solutions of magnesium sulphate, and although it is almost entirely collected around the nucleus at the centre of the cell, the latter still remains turgid.

I am of opinion that de Vries' view that the turgidity of the cell is mainly dependent on the presence of certain osmotically active substances in the sap, of an acid nature, requires some further qualification, for my own results agree rather with those of Schwartz, since I find that turgid cells may possess either an acid or an alkaline sap. Thus, in *Drosera* itself, the cells of the tentacles have an acid, and those of the petals of the flower an alkaline reaction.

Finally, the property of contractility, which I have established for the irritable cells of *Drosera* and *Mimosa*, and for the less specialised cells of *Mesocarpus*, is, I believe, a property which is possessed, in a greater or less degree, by all the actively living cells which constitute the tissues of plants. The important bearing of these results on all phenomena of movement and growth is sufficiently obvious.

WALTER GARDINER, Cambridge.

THE REPLUM IN CRUCIFERAE.—What is the replum? Writers on systematic botany use the term for the framework of the fruit, left after the fall of the valves, across which the septum stretches. In Continental and American text-books the term is also used in this sense. In most British text-books the term is applied to the septum itself. The purpose of this note is to point out which of those uses is the correct one.

The word was introduced by Brassai in Flora, Jahrg. XVI, Bd. I, p. 313. In a note to a discussion of the morphology of the capsule in Papaveraceae, he remarks of the fruit in Cruciferae that it is to be regarded as a capsule with two parietal placentas, the walls of which are cut out on two opposite sides between the placentas. The portions so cut out—his *assumenta*, our *valves*—are larger or smaller in different cases and may indeed be non-existent, and a series may be traced from *Thlaspi*, in which they are large, to *Bunias*, where they are absent. The whole remaining portion of the capsule after removal of the valves is the *replum*. Although he does not specially mention the septum, it is clear from the whole context that Brassai introduced the term for the framework across which the septum stretches, and not for the septum; and this would correspond with the original meaning of the word, viz., 'the upright rail fixed in the centre of the frame of a door-case in order to guard the crevice formed by the junction of two valves' (White and Riddell). The

use of the word in most of our text-books in Britain is therefore wrong, and, so far as I can discover, the error was first made by Henfrey in his Outlines (1847), whence it has been copied into other books.

According to Lecoq and Juillet the term *repletum* was applied by Richard to a pericarp such as that of Orchideae, in which the valves fall away leaving a framework of cohering delicate threads. I have not been able to find the word in Richard's works, but its use by him, involving the same idea as that conveyed by Brassai's term, would be prior to the paper of Brassai referred to above.

ISAAC BAYLEY BALFOUR, Oxford.

NOTICES OF BOOKS AND PAPERS.

UEBER DIE CULTUR FLECHTENBILDENDER ASCOMYCETEN OHNE ALGEN: von ALFRED MOELLER. (Untersuchungen aus d. bot. Inst. d. Königl. Akad. zu Münster-in-Westfalen.) 8vo. Pp. 52.

In this paper the author gives the results of cultures of the spores of a number of crustaceous lichens which in several respects form a valuable contribution to our knowledge of the development of the lichen-thallus. The paper begins with a well-written summary of the views of previous writers on the nature of lichens, and the results of their cultures of spores and gonidia. Believing that little more light on this much-discussed subject can be obtained by cultures of gonidia alone, or by attempts to produce lichens synthetically by the use of gonidia and spores, he turned his attention to the culture of spores in suitable nourishing media. The species studied were *Lecanora subfusca*, L., *Thelotrema lepadinum*, Ach., *Pertusaria communis*, D. C., *Buellia punctiformis*, Hoffm., *Lecidella enteroleuca*, *Opegrapha subsiderella*, Nyl., *O. vulgata*, Ach., *O. varia*, Pers., *Graphis scripta*, L., *Arthonia vulgaris*, Schaer., *Calicium parietinum*, Ach., *C. trachelinum*, Ach., *C. curtum*, Borr., and *Verrucaria muralis*, Ach., which, it will be seen, include representatives of nearly all the tribes of lichens.

The original account can hardly be presented in a condensed form, for the details given, although numerous, are important. Briefly stated, two important facts have been brought out by the author. In the first place, the prevailing opinion that the hyphae coming from germinating lichen-spores perish in a short time unless gonidia are present is shown to be false. By using proper culture media, and observing proper precautions, the hyphae from the spores of the species named continued to grow for more than three months, and, at the date of publication, many of the cultures were still in good condition. The hyphae produced small characteristic thalli, without any trace of gonidia however. At the time of writing none of them had produced apothecia, although in the case of *Graphis scripta* small bodies had appeared which turned violet on the application of iodine, and

looked like the beginnings of either apothecia or pycnidia, more probably the latter. In some species, as *Lecanora subfusca*, the hyphae radiate from the spore in a horizontal plane, forming what was called by the older lichenologists a hypothallus. Later on, the branches of the hyphae are vertical, and a proper thallus arises in which, in some species, a proper cortical layer is formed. The very slow rate of growth is shown by the fact that, at the end of three months, the thalli of *L. subfusca* were only from 1·5 to 2 mm. in diameter, while in *Opegrapha subsiderella* the growth was much slower. Closely related species, however, vary very much in their rate of growth, for, while in *Opegrapha* it was extremely slow, in *Graphis scripta* it was comparatively rapid.

The second point of interest is that, in several of the species studied, the spermatia when cultivated gave out hyphae which formed thalli similar to those produced by the spores. On this point Dr. Moeller's observations are conclusive, although it is perhaps a little premature to say that the spermatia of all lichens are of the nature of conidia and will germinate under favourable conditions. Analogy would lead us to suppose that this is the case, but in a question of this kind analogy must be supplemented by corroborative testimony. Our present knowledge of the function of the spermatia of lichens rests almost wholly on the classical researches of Stahl [1], on the reproduction in *Collemaceae*. In this group of lichens, according to Stahl, the spermatia attach themselves to the tip of a trichogyne, at the base of which is a carpogonium. As the development of the carpogonium into the apothecium appears to follow the contact of the spermatia with the trichogyne, the spermatia may reasonably be assumed to be the fertilizing male element. Dr. Moeller does not think that this is conclusively proved by Stahl. It is to be regretted that none of the species studied by Dr. Moeller belong to the *Collemaceae*, so that for this group we must still fall back on the researches of Stahl.

With regard to the lichens of other groups, the present observations show conclusively that the spermatia are conidial in nature and not male bodies. In *Buellia punctiformis*, and in all the species of *Opegrapha* and *Calicium* above named, the spermatia produced hyphae which developed into thalli. A comparison of the results obtained by sowing the spores and the spermatia showed that there was no per-

[1] Ueber die geschlechtliche Fortpflanzung der Collemaceen. Leipzig, 1877.

ceptible difference in the two cases. The cultures of *Calicium parietinum* were especially interesting. The spores germinated and grew with comparative rapidity, and in five or six weeks black spots appeared in the thalli, which in less than a week developed into pycnidia [1] containing conidia, and, from the conidia thus obtained, new cultures were made which produced a second crop of conidia, thus giving 'for the first time incontestable proof of the connection of ascospores and conidia in a lichen.' In *Calicium trachelinum*, which grows more slowly than *C. parietinum*, there are two conidial forms, one borne on arthrosterigmata, the other on simple sterigmata, as first shown by Lindsay in *Calicium*, and both germinate and produce thalli as well as the ascospores.

We hope to hear again concerning the further development of the thalli still growing when the present paper was completed, and should be glad if the author could furnish illustrations, although, from the nature of the material, it must evidently be difficult to provide characteristic figures.

W. G. F.

UEBER DIE ABHÄNGIGKEIT DER ASSIMILATION GRÜNER ZELLEN VON IHRER SAUERSTOFFATHMUNG, UND DEN ORT WO DER IM ASSIMILATIONSACTE DER PFLANZENZELLE GEBILDETE SAUERSTOFF ENTSTEHT: von **N. PRINGSHEIM** (Separatabdruck aus Sitzungsber. d. k. Preuss. Akademie d. Wiss. zu Berlin, xxxviii. 1887).

Some account of the observations described and discussed in this paper was given by Professor Pringsheim at the recent meeting of the British Association at Manchester, so that at least the general results at which he has arrived are already known to many English botanists. But, in view of the importance of the subject, it may not be superfluous to give a brief notice of the method employed and of the results attained, as well as a discussion of the inferences which Professor Pringsheim draws from his facts.

The object of the investigation was to determine (1) what relation,

[1] The author, regarding the spermatia as conidia, uses the term pycnidia to include spermogonia as well as the pycnidia proper which are found in some species of lichens.

if any, exists between the assimilation of carbon by gree
the supply of free oxygen, and (2) to ascertain the seat of
oxygen evolved in connection with the assimilation of
order to attain this object, it was essential to possess
within and without the living cell, of determining the pres
oxygen. For the latter purpose the Bacterium-method was
for the former, Prof. Pringsheim devised a method of his o
the observation of the rotation or circulation of the protop
cell. Since it is known that these movements depend up
of free oxygen, it is clear that their arrest or resumption m
as an indication of the absence or presence of this gas. It
essential to control the composition of the atmosphere.
done by observing the cells in a closed chamber through
rent of the required mixture of gases was kept passing.
used were the leaflets of *Chara*, the terminal cell being
observed. They were examined suspended in a hangi
water.

The general nature of the experiments may be briefly
as follows:—

1. When the cell was deprived of a supply of free oxyge
ture of gases passing through the chamber consisting o
with 10 % carbon dioxide (in some cases 3–5 %), and
darkness, the rotation of the protoplasm was arrested soo
(2–10 hours). Prolonged exposure in the atmosphere of
caused death (Asphyxia); but when oxygen was admit
chamber soon after the protoplasmic movements had
movements were resumed.

2. When a cell in which rotation had just ceased was
light in the same atmosphere (CO_2 and H), the rotation w
sumed: but was readily resumed on admitting air into th
Hence it appears that the period of existence in an atmos
taining no free oxygen which causes the arrest of rotation, i
a condition of the protoplasm in which it is incapable of a
carbon. This condition of 'nutritive incapacity' (*E*
ohnmacht), Pringsheim terms *Inanition*. No evolution
from a cell in this condition can be detected by the
method.

3. When a cell was kept continuously exposed to light in
sphere of CO_2 and H, rotation eventually ceased, much as in

and the state of inanition was induced. In most cases the evolution of oxygen by the cell, as determined by the Bacterium-method, ceased much sooner than the rotation; but in many instances the converse was the case.

The bearing of these facts upon the relation between the process of assimilation and the supply of free oxygen is obvious. It is clearly proved by these observations, assuming the soundness of the methods, that this process of assimilation can only be carried on when the protoplasm is adequately supplied with free oxygen. In this conclusion Professor Pringsheim agrees with de Saussure [1], but differs from Boussingault [2], who came to the conclusion that the absorption and decomposition of carbon dioxide by leaves is quite independent of free oxygen. The discrepancy between the results of Boussingault and of Pringsheim appears to be easily explicable in favour of the latter. It does not appear that, in Boussingault's experiments, there was any provision for a *continuous current* of the irrespirable gas or mixture of gases such as there was in those of Pringsheim. Hence, in the former, the oxygen gradually accumulated in the receiver, and consequently their value is vitiated.

Professor Pringsheim draws from these facts the further conclusion that, in the process of assimilation of carbon, no oxygen is set free in the interior of the cell, but that a substance is formed in the cell which escapes by osmosis, and undergoes decomposition at the surface, free oxygen being one of the products. He argues that if free oxygen were evolved in the interior of the cell, it would be impossible for the arrest of rotation and the condition of inanition to supervene whilst the cell is exposed to light in an atmosphere containing carbon dioxide; and, on the strength of this argument, he indulges in some severe strictures on the 'gas-analytical' method by means of which most of the existing knowledge of the process of assimilation of carbon from carbon dioxide has been obtained. He urges that the decomposition of carbon dioxide and the evolution of oxygen are two distinct processes, as distinct as the absorption of oxygen and the evolution of carbon

[1] 'Nous venons de reconnaître que le gaz acide carbonique ajouté artificiellement dans de très petites proportions à l'atmosphère des plantes, est utile à leur végétation au soleil; mais il n'exerce cette action bienfaisante qu'autant que cette atmosphère contient du gaz oxygène libre.' (De Saussure, Recherches Chimiques, 1804, p. 33.)

[2] Boussingault, Etudes sur les fonctions des feuilles, Comptes Rendus, lx, p. 862, 1865; also, Agronomie, Chimie Agricole, &c., iv, 1868, pp. 301–2.

dioxide in respiration. In support of this view he cites cases in which he has observed that parts of plants, whether or not containing chlorophyll, evolve oxygen in darkness (indicated by the Bacterium-method) as they gradually die; in which there is a sort of 'intramolecular' evolution of oxygen, just as there is an 'intramolecular' evolution of carbon dioxide in parts of plants when cut off from a supply of free oxygen.

This line of argument is, however, by no means conclusive. One of his own facts militates strongly against it; the fact, namely, that, in cells continuously exposed to light, the rotation continued, in most cases, for a longer time than the evolution of oxygen, which would seem to indicate that oxygen was set free in the interior of the cell for some time after it had ceased to be evolved at the surface. This fact might be explained away by assuming that the rotation is maintained by intramolecular respiration, but such an explanation is quite at variance with what is known as to the physiology of these protoplasmic movements, and it is rejected by Professor Pringsheim himself.

Again, the phenomenon which this new theory is especially designed to explain, the phenomenon of the gradual arrest of movement and the induction of inanition in a cell exposed continuously to light in an atmosphere of hydrogen and carbon dioxide, may be explained, and apparently in a satisfactory manner, by means of a less hazardous assumption. It involves no great stretch of the imagination to suppose that, in consequence of there being a continuous current of hydrogen and carbon dioxide passing through the chamber, the oxygen was removed from the cell more rapidly than it was produced, so that eventually no free oxygen was present, and that then arrest of movement and inanition were induced.

It is true that, in some cases, the phenomenon necessary to prove the truth of the theory was observed; the phenomenon of the arrest of the rotation in the cell *before* the cessation of the evolution of oxygen at the surface, as indicated by the Bacterium-method. But these cases constitute only a minority of the observations. It is therefore impossible to accept the second of Professor Pringsheim's conclusions without more convincing evidence.

S. H. V.

DAS PFLANZENPHYSIOLOGISCHE PRAKTIKUM: ANLEITUNG ZU PFLANZENPHYSIOLOGISCHEN UNTERSUCHUNGEN FÜR STUDIRENDE UND LEHRER DER NATURWISSENSCHAFTEN: von Dr. W. DETMER, Professor an der Universität Jena. Jena (Gustav Fischer), 1888.

A 'Praktikum' or Laboratory course in the Physiology of Plants was undoubtedly needed, and Professor Detmer's volume is well adapted to fill up this hiatus in the student's library. The author has been in the habit of conducting a physiological class at Jena, and has thus had experience which enables him to put his material in a practical form. The book is not simply a laboratory guide, not a mere skeleton of categorical instruction, but contains a certain modicum of discussion and connecting matter, after the manner of lectures.

The instructions to the student have the merit of being obviously taken from the author's personal experience. This is of course indispensable in such a book; but when, as in the present instance, the personal tone is strongly marked, the descriptions gain a vitality which is not only instructive and encouraging to the student, but also renders the author's pages more readable to those who have not the means of working through the whole course. He is especially to be commended for the care with which he has given minute instructions in matters of manipulation. Thus, for instance, he gives a careful description of the best method of marking growing organs at equal intervals. Again, he attends to such minutiae as that the seeds of *Vicia Faba* should be sown with the micropyle downwards, whereas those of *Phaseolus* should have the cotyledons horizontal. Where so much is good we do not greatly care to point out what might be better. There is, however, a fault running more or less throughout the work, which might be amended in a future edition. The book is either too long or too short. His laudable desire to make the course complete, has led the author into a certain kind of incompleteness and want of balance. Detailed points which should have been omitted or more fully dealt with are treated in an incomplete manner, which cannot be commended. For instance, the section on the mechanical analysis of soil, with its details about the 'Schlämm-cylinder,' and the meshes of sieves, might well have been omitted. The space and time saved by such omissions might have been given

to more important points,—for instance, to the auxanometer,—an instrument rather scantily discussed. A similar criticism may be made as to the introduction of structural details. The student might have been referred to special treatises for such subjects as periclinal and anticlinal lines, or the transverse section of the dicotyledonous stem, and the incomplete discussion of these points might have been omitted. With a little care in this direction, the author might easily effect improvements in what, as it stands, is an excellent book.

F. D.

EINLEITUNG IN DIE PALÄOPHYTOLOGIE VOM BOTANISCHEN STANDPUNKT AUS. Bearbeitet von H. GRAFEN ZU SOLMS-LAUBACH. Leipzig, Felix, 1887.

It has been known for some years past that Graf zu Solms-Laubach was engaged in the preparation of a general work on Paläobotany, and its appearance has been looked for with no little interest, especially in Britain, where Fossil Botany has found so many of its most zealous and successful students. General treatises hitherto published in this branch of science have given prominence either to the geological or to the systematic aspects of the subject, and it has been left to Graf zu Solms-Laubach to approach it in this book from a distinctly new standpoint, that of the morphological botanist. We do not require to say that he is peculiarly well fitted for the task he has imposed upon himself; the result is a book worthy of his authorship.

The difficulties which most botanists have found in acquiring information on the subject of Paläophytology may be traced to two primary sources; in the first place, too many of the workers who have dealt with the fragmentary remains of an old vegetation have not been fitted by any previous botanical training for the work, and consequently their descriptions and identifications are alike untrustworthy; in the second place, solitary minute fragments from isolated districts are often the only foundation for important statements or hypotheses, which, from the evidence supplied, it is hazardous either to accept or refute. Hence the only plan for obtaining a satisfactory basis of knowledge is an examination of all the type specimens in their several localities, and this is manifestly out of the question for the majority of botanists. Now, this is just what Graf zu Solms-Laubach

has done, and his book is founded in great measure upon this experience. He has spent a considerable portion of his time for several years visiting the collections of the most prominent workers, and has passed through his hands most of the important types described by authors; and so the whole subject has been sifted through one mind and been criticised by a trained and expert botanist, who has applied to each and all of the specimens submitted, the test of his own acute observation and logical reasoning; and we have now presented to us a treatise on the subject of some homogeneity, and stamped throughout with the consistent method of one competent critic.

The book begins with an introductory chapter in which the imperfection of the geological record is touched upon, and the various modes of preservation of plant remains as fossils is fully set forth, a considerable portion of the chapter being devoted to the question of the origin of coal, the modified allocthonous view of Grand-Eury being that to which the author inclines. Then comes a chapter on Thallophyta and Bryineae; the most interesting points in it being the clear exposition of the structure and relations of the Mesozoic Siphoneae, formerly classed with the Foraminifera, and the judicial summary of the dispute regarding the plant-nature of many Palaeozoic impressions. Chapter III deals with Coniferae and IV with Cycadeae, and in the latter the author makes a point of the structure and relationship of *Bennettites*, seeking to establish it as type of a group between Gymnosperms and Angiosperms. Next follows a chapter on the interesting extinct Cordaiteae, and one on allied forms such as *Dolerophyllum Cannophyllites*, and others; and then we come to Chapter VII on Filices, containing a remarkably clear and full statement of what is known of their morphology. Chapters VIII and IX contain accounts of Equisetaceae and the much discussed *Traquairia* and *Sporocarpon*, and of *Lycopodites*, *Psilophyton*, and others, and the following chapters take up the subjects of Lepidodendreae, Sigillarieae, and *Stigmaria*. No more interesting passages will be found in the book than the discussions of the relations and affinities of these—the author staunchly upholding the view that *Stigmaria* belongs, as an underground part, to both Lepidodendreae and Sigillarieae. In Chapter XIII the Calamarieae are taken in hand, and the grouping of the forms into Archegoniate Calamiteae and Gymnospermous Calamodendreae is held to be

untenable. Subsequent chapters deal with Sphenophylleae and a number of other forms which our author regards as of doubtful relationship. A bibliographical list concludes the volume.

Readers will miss an account of the Angiosperms, but these, as the author explains in the introductory chapter, would have been of little interest from the point of view which he has adopted with reference to the whole subject; and it is on account of this omission that the work is simply called an introduction to Palaeophytology.

The book as a whole is an able critical digest of the field over which it travels, and the specimens, descriptions, and hypotheses of writers are examined with thorough impartiality. Approval of the views of a writer on one point in one paragraph often prefaces dissent from the same writer on another point in the succeeding paragraph; and acknowledgment by our author of the kindness of a worker in submitting an original specimen for examination is not infrequently followed by an expression of regret that he is unable to agree with him in his interpretation of its facts. All is written however with a charming frankness, good temper, and courtesy.

Of course, Graf zu Solms-Laubach's views will not be altogether accepted by Palaeophytologists. On some points he has undoubtedly been led into wrong assumptions;—to note only one point, which we hope will be placed beyond all doubt by a paper in an early number of the ANNALS OF BOTANY, *Pachytheca* is an Alga, although Graf zu Solms-Laubach is inclined to assign it to the inorganic kingdom;—but the genuineness of his attempts to get at the truth and unweave the tangled veil that invests so much of the subject is everywhere manifest, and even his wrong-going will do good by bringing out further evidence to prove that such is the case.

One feature that will strike all English readers of the book is the attention that has been paid to works in English. This was inevitable in any honest book on Fossil Botany, but it is none the less satisfactory to find the work of Witham, Lindley and Hutton, Hooker, Binney, Williamson, Carruthers, Dawson, and others, so fully acknowledged, because a tendency of an opposite kind prevails in too many modern German works.

The book is one of great value and importance. We are greatly mistaken if it does not give a new impetus to the study of fossil plants, for it will enable any botanist to obtain an insight into the

present state of the more important issues of the science. It might have been of interest to readers of the ANNALS OF BOTANY had we entered in more detail into the subjects of the several chapters, but we content ourselves, for the present, with this brief notice of the book calling the attention of botanists to it, for we are glad to be able to say that Mr. Garnsey is adding another to the obligations under which the English-speaking botanical world already lies to him for his indefatigable labour in giving it access to standard German works, and is engaged in the preparation of a translation of the book which will be published by the Clarendon Press. It is to be hoped that in the course of the year the book in English dress will be within the reach of all English students, when they will be able to appreciate better than from a review the sterling excellence of Graf zu Solms-Laubach's work.

I. B. B.

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BOTANICAL NECROLOGY FOR 1887.

JOHAN EHRHART ARESCHOUG[1]. Born at Göteborg, September 16, 1811. Died at Stockholm, May 7, 1887. Educated at University of Lund. Docent at University of Lund 1839. Lecturer on Natural History at Gymnasium of Göteborg 1841. Adjunct at University of Upsala 1849. Extraordinary Professor of Botany at the University of Upsala 1858. Ordinary Professor of Botany at University of Upsala 1859–1876. Biographical notice by O. Nordstedt in Botaniska Notiser, 1887. Published :—

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[1] The Editors are indebted to Prof. F. W. C. Areschoug, of Lund, and Prof. Blytt, of Christiania, for information about Prof. J. E. Areschoug.

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JEAN BAPTISTE BOUSSINGAULT. Born at Paris, February 2, 1802. Died at Paris, May 11, 1887. Educated at the School of Mines, St. Etienne, 1822. Professor at the School of Mines, Bogota (South America). Officer in the army of Columbia during the War of Independence of this State. Professor at the Faculté des Sciences, Lyon, 1835. Professor at Paris, 1837. Member of the French Academy, 1839. Professor of Agriculture at the Conservatoire des arts et métiers, 1845 (he held this appointment until his death, but only as an honorary post during the later years). Biographical notice by Pringsheim in Berichte der deutschen bot. Gesellschaft, Generalversammlungsheft, 1887. Published:—

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DIDRIK FERDINAND DIDRICHSEN[1]. Born at Copenhagen, June 6, 1814. Died at Copenhagen, March 19, 1887. Surgeon and Botanist on the Galathea 1845–47. Librarian at the Botanic Garden in Copenhagen 1851. Docent in the University of Copenhagen 1858–75. Professor of Botany in the University of Copenhagen 1875–85. Biographical notice by Nordstedt in Botaniska Notiser, XXIII (1887), and by Eug. Warming in Botanisk Tidsskrift, XII (1887). Published:—

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[1] The Editors are indebted to Prof. Warming, of Copenhagen, for information about Prof. Didrichsen.

AUGUST WILHELM EICHLER[1]. Born at Neukirchen (Hessen) April 22, 1839. Died at Berlin, March 2, 1887. Educated at Gymnasium Hersfeld and University of Marburg. Assisted Martius at Munich with Flora Brasiliensis, 1861–1868. Privatdocent at Munich, 1865–1871. Professor of Botany and Director of Botanic Garden, Graz, 1871–1873, at Kiel, 1873–1878, at Berlin, 1878–1887. Editor of Flora Brasiliensis from date of Martius's death in 1868 to 1887. Co-editor of Jahrbuch des Königlichen botanischen Gartens und des botanischen Museums zu Berlin, 1882–1887. Biographical notices by Tschirch in Flora, 1887, No. 16; C. Müller and J. Urban, in Bot. Centralblatt, XXXI, XXXII (1887); R. Schumann, in Berichte der deutschen bot. Gesellschaft, Generalversammlung, 1887. Published:—

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WILLIAM FERGUSON. Born July, 1820. Died at Colombo, Ceylon, July 31, 1887. Surveyor. Lived in Ceylon from 1839. Biographical notice in Journal of Botany, October, 1887. Published:—

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JOHN FRANCIS JULIUS VON HAAST. Born at Bonn, May 1, 1824. Died in New Zealand, August 16, 1887. Educated at the Grammar School of Bonn and Köln, and at the University of Bonn. Went to New Zealand in 1858 as agent for a business firm to report upon its fitness for emigration from Germany. Afterwards accompanied Hochstetter in his explorations of New Zealand, and then himself explored several districts at request of Colonial Government. Head of Geological Survey of New Zealand, 1861–1887. K.C.M.G. 1886. Biographical notice in Nature, XXXVII. Published:—

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And many geological and zoological papers.

ALBERT KELLOGG. Born at New Hartford, Connecticut, December 6, 1813. Died at Alameda, near San Francisco, March 31, 1887. Educated at Medical College, Charleston, South Carolina, and Lexington, Kentucky. M.D. With Audubon explored parts of America. Settled in California in 1849. One of founders of Californian Academy of Sciences. Made extensive collections in California, on the river of Alaska and elsewhere. Biographical notice by Greene in Pittonia I (1887). Published:—

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JEAN JACQUES KICKX.[1] Born at Ghent, January 27, 1842. Died at Ghent, March 27, 1887. Educated at the Universities of Ghent and Bonn. D.Sc. 1863. Professor of Botany in the University and Director of the Botanic Garden and of the School of Horticulture of Ghent 1867. President of the Société royale botanique de Belgique 1879. Rector of the University of Ghent 1887. Chevalier de l'ordre Léopold. Biographical notice;

[1] The Editors are indebted to Dr. J. Macleod, of Ghent, for information about Prof. Kickx.

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VINCENZ FRANZ KOSTELETZKY[1]. Born at Prague, March 13, 1801. Died at Dejwitz, near Prague, August 18, 1887. Educated at the University of Prague. M.D. 1824. Assistant at the Botanic Garden of Prague, 1824. Deputy Professor of Botany at the University of Prague 1828–35. Professor of Botany at the University and Director of the Botanic Garden of Prague, 1835 to 1872. Biographical notice by Wilkomm in Bot. Centralblatt, XXIII (1888). Published:—

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CORNELIUS MARINUS VAN DER SANDE LACOSTE[2]. Born at Dordrecht, March 5, 1815. Died at Amsterdam, January 15, 1887. Educated at the University of Utrecht. M.D. Early retired from practice and devoted himself to Bryology. Published:—

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[1] The Editors are indebted to Prof. Wilkomm, of Prague, for information about Prof. Kosteletzky.

[2] The Editors are indebted to Prof. Oudemans, of Amsterdam, and Prof. Suringar, of Leiden, for information about Dr. Lacoste.

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Besides many identifications of plants collected during the excursions of the Dutch Botanical Society which appear in the Nederlandsch Kruidkundig Archief and elsewhere.

EDWIN LEES[1]. Born at Worcester, 1800. Died at Worcester, October 21, 1887. Printer and Stationer in Worcester, early retired from business. One of Founders of Worcester Nat. Hist. Soc. and of Worcestershire Naturalists' Club. Editor of Malvern News and Journal, 1861. Biographical notice in Journal of Botany, December, 1887. Published:—

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Also many articles on the Natural History of Malvern and its vicinity in the Malvern News and Journal under his own name, and the assumed one of Alwynus Malverine.

HUGO LOJKA[1]. Born at Gelsendorf (Galizia), January 6, 1844. Died at Budapest, September 7, 1887. Teacher of Botany in Higher National Girls' School, Budapest. Published:—

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EZRA MICHENER. Born at London Grove township, Chester Co., Pa., November 24, 1794. Died at Tonghkenamon, Chester Co., Pa., June 25, 1887. Collector of Cryptogamous plants, especially Fungi. Biographical notice in Journal of Mycology, III (1887). Published:—

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NORBERT LOUIS MICHOT[1]. Born at Thuin, February 4, 1803. Died at Mons, April 9, 1887. Educated at the College of Thuin and the Seminary of Tournay. Abbé at Mons from 1840. Almoner of the Carmelites. Biographical notice with funeral oration by M. Paul Laduron, printed at Mons by Dequesne-Masquillier. Published:—

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THOMAS MOORE[2]. Born near Guildford May 21, 1821. Died at Chelsea January 1, 1887. Gardener in the Botanic Garden, Regent's Park. Curator of the Botanic Garden of the Society of Apothecaries at Chelsea, 1848–1887. Co-editor of Gardener's Magazine of Botany 1850–51; of Garden Companion and Florist's Guide, 1852; of Floral Magazine, 1861; of Gardeners' Chronicle, 1866–1881; of Orchid Album, 1881–87. Editor of Florist and Pomologist, 1868–74. Biographical notice in Gardeners' Chronicle, ser. 3, Vol. I (1887), and in Journ. of Bot. XXV (1887). Published:—

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Also descriptions of new ferns and other plants, and many short articles, in the periodicals with which he was connected.

LOUIS PIRÉ[1]. Born March 3, 1827. Died at Spa, 16 July, 1887. Honorary Professor at l'Athénée, Brussels, 1854–87. Editor of the Bulletin de la Société Linnéene de Bruxelles, 1872–87. Published:—

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HENRY WILLIAM RAVENEL. Born at St. John's, Berkley, South Carolina, May 19, 1814. Died at Aiken, South Carolina, July 17, 1887. Graduate of South Carolina College. Planter residing at St. John's, S. C., 1832–1853; at Aiken, S. C., 1853–1887. Botanist to Texas Commission to investigate the cattle disease. At one time Agricultural editor of the Weekly News and Courier. Biographical notice by Prof. Farlow in the Botanical Gazette, Vol. XII (1887), p. 194. Published:—

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KIRBY TRIMMER. Born at Poplar, Middlesex, December 22, 1804. Died at Norwich, October 9, 1887. Educated at Oxford. Vicar of St. George Tombland, Norwich. Biographical notice in Journal of Botany, December 1887. Published:—

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HEINRICH WAWRA.[1] Born at Brünn, February 2, 1831. Died at Baden, near Vienna, May 24, 1887. Educated at Brünn Gymnasium and University of Vienna. M.D. Surgeon in Austrian Navy, 1856. Visited, in Austrian ships, various countries and made botanical collections. Accompanied the Austrian exploring expedition to Eastern Asia. Ritter von Fernsee, 1873. Co-editor of Wiener Illustrirte Gartenzeitung from 1886. Biographical notice in Wiener Illustr. Gartenzeitung, 1887, and in Flora, LXX (1887). Published:—

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HEINRICH GEORG WINTER. Born at Leipzig, October 1, 1848. Died at Connewitz, near Leipzig, August 16, 1887. Educated at the Thomasschule in Leipzig. Apprentice to bookseller. Studied at Leipzig and Munich. Assistant to Prof. Kraus, at Halle a. S. 1873. Docent in Botany at Polytechnikum and University of Zürich 1875. Co-editor of Hedwigia, 1871–79 Editor of Hedwigia, 1879–1887. Biographical notice by Magnus in Ber. d. deutsch. bot. Gesellsch. Generalversammlung. Band V (1887). Published:—

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GEORG CHRISTIAN WITTSTEIN.[1] Born at Münden (Hannover), January 25, 1810. Died at Munich, June 1, 1887. Educated at the Gymnasium of Münden. Pharmaceutical chemist for about 10 years. Studied at the University of Munich. Ph. D. 1840. Assistant to Professor Buchner until 1851. Professor of Chemistry, etc. at Ansbach 1851. Resigned this appointment in 1853 and founded a technical school at Munich, which was under his directorship for 26 years. Biographical notice in Chemiker-Zeitung, XI (1887). Published:—

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